University of Alberta

Mountain pine beetle infestation risk: interactions of population phase, host vigour and spatial aggregation

By

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ABSTRACT

Pine trees attacked by mountain pine beetles *(Dendroctonus ponderosae)* exhibited positive spatial association up to 39 m. MPBs typically attacked trees in the immediate neighbourhood of a focal tree and aggregation declined with increasing distance. The patchy distribution of attacks may result from conspecific attraction of MPBs by means of aggregation pheromones. The spatial extent of the attraction of beetles to existing infestation centres increased with beetle population size. When infestation was severe, host depletion inhibited aggregation over large spatial scales. The proportion of infested neighbours and tree diameter were the most important factors determining infestation risk. Beetle population size also determines the vigour class of preferred hosts. When the population was small, beetles were restricted to trees with smaller diameters. Crown length reduced the risk. Beetles appear to balance losses due to a greater defence capacity in more vigorous trees with the advantages of greater phloem thickness and quality.

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CHAPTER 1

INTRODUCTION

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins, MPB) is a native insect in Western North America that attacks mature lodgepole pine (*Pinus contorta* var. *latifolia*), the predominant timber species in British Columbia (BC) (Council of Forest Industries, 2003). Over the past 40 years the range of mountain pine beetle has expanded, possibly due to changes in the area of climatically suitable habitat (Carroll *et al.*, 2004; Taylor *et al.*, 2006). It is thought that fire suppression in combination with climate change (Carroll *et al.*, 2004; Taylor & Carroll, 2004) has recently resulted in the largest insect epidemic in BC's history. Aerial overview surveys in 2005 estimated 8.7 million hectares damaged by MPB (Westfall, 2005). By 2003 the infestation in BC had caused losses in lumber products worth $18 billion (Patriquin *et al.*, 2005) due to chemical and morphological changes in infested wood (Woo *et al.*, 2005). There are also aesthetic changes as symbiotic fungi associated with MPBs stain infested wood blue (Ayer *et al.*, 1986; Yamaoka *et al.*, 1990; Solheim, 1995). The epidemic is expected to last for another 10 years, causing 80% losses of the merchantable pine volume (Eng *et al.*, 2004). Research on the MPB is essential to inform policy enacted to minimize the impact that large-scale epidemics have on economics and natural systems in BC.

1. ECOLOGICAL IMPLICATIONS OF THE INFESTATION

Aside from the impacts on society, epidemics also influence forested systems by initiating gaps which alter the forest structure and composition. In the absence of fire, insect outbreaks may control inter-fire stand dynamics that determine spatial patterns, age structure and species composition of forests (Parish *et al.*, 1999). The reduction in fire-return intervals in British Columbia has resulted in mature, densely stocked pine dominated stands (Taylor *et al.*, 2006). MPB can be considered as a thinning agent of overstocked stands with strong competition, that are growing slowly and that are therefore highly susceptible (Mitchell *et al.*, 1983; Waring & Pitman, 1983). By opening the canopy, suppressed trees are released (Worrall *et al.*, 2005) and gaps are opened for colonization by shade-intolerant species where environmental conditions permit. Understory biomass increases exponentially with disturbance severity caused by MPB infestation, providing forage and browse to livestock and wildlife (Stone & Wolfe 1996). Species richness in understory plants such as grasses, trees and shrubs with a greater abundance of fruit occurs at intermediate disturbance levels. Increased understory growth adds a large quantity of near continuous ground fuels, such that a severe outbreak may create conditions more favourable for high intensity fires (Turner *et al.*, 1999). The MPB is thus an important agent that affects every aspect of forest ecosystems, including regeneration, biodiversity and habitat quality for wildlife.

2. MPB ECOLOGY

A recent review of MPB biology provided a detailed overview of the MPB life-cycle and ecology (Safranyik & Carroll, 2006). The following sections are intended as a brief introduction to the aspects of MPB ecology that are relevant to the questions examined in this thesis.

2.1. PHENOLOGY

MPBs preferentially attack trees with large diameters since large thick barked trees contain the thickest phloem, their critical food source (Amman, 1969; Cole, 1973; Amman & Pace, 1976; Berryman, 1976; Amman & Cole, 1983; Shrimpton & Thompson, 1985). The number of emerging adults increases with phloem thickness and diameter (Amman, 1972; Safranyik *et al.*, 1975; Berryman 1976; Amman & Pasek, 1986). Large trees also provide a greater surface area for beetle colonization and multiplication (Waring & Pitman, 1983) and thicker bark provides greater insulation against cold in winter (Cole, 1973). Thick bark also has more niches in which beetles brace themselves while chewing an entrance hole (Safranyik & Vithayas, 1971). Both females and males construct the egg gallery by feeding on the phloem and clearing the tunnel from boring dust (Reid, 1962). Females may lay over 200 eggs (Reid, 1962), but often produce less (for details see Safranyik & Carroll, 2006). The time required for eggs to hatch depends on temperature. Safranyik and Whitney (1985) observed an average time of 34 and 7.4 days for eggs to hatch at 10°C and 20°C, respectively.

Beetles typically overwinter as third- or fourth- (i.e. last) instar larvae which resume development in the spring (Amman, 1973). Pupation occurs in early summer, followed by the teneral adult stage during which the soft immature adults that are not yet able to reproduce mature under the bark. Mature adults emerge in late July or early August. Advanced life-stages (larval instars III, IV and pupae) require higher temperature for development than eggs, instar I or instar II such that each life-stage has a specific optimal temperature regime and threshold for development (Bentz *et al.*, 1991). This inherent mechanism synchronizes larval instar molts and adult emergence. Evolution of this life-history strategy maximizes MPB fitness in a constantly changing environment; higher temperature thresholds in larval instars III and IV prevent progression to advanced life-stages that are less cold tolerant (Bentz *et al.*, 1991). Since third- and fourth- instar larvae do not develop at cool temperatures whilst eggs and first- and second-instar larvae continue to develop, late-hatching eggs are able to catch up. This ensures temporally synchronized adult emergence that enables mass attacks (Bentz *et al.*, 1991). A mass-attack occurs when beetles concentrate their attacks on one particular tree (see Section 2.2 and 2.3 for details).

2.2. DISPERSAL AND AGGREGATION

It is well established that MPBs aggregate in response to pheromones produced by conspecifics to focus attacks on one large tree, thereby exhausting its defence capacity (see Section 2.3). Mass-attacking a large tree maximizes reproductive output since larger trees produce more and larger beetles (Reid 1963; Amman, 1972; Cole, 1975; Berryman, 1976; Waring & Pitman, 1983). Pitman *et al.* (1968) showed that hindguts of MPB females, in contrast to other *Dendroctonus spp*. do not contain much *trans*-verbenol, an aggregation pheromone, prior to penetrating the bark of their host and that they produce it when feeding on its bark. Pheromones are only found in adult MPBs after host colonization (Hughes, 1975). Vité and Pitman (1968) also showed that extensive feeding in new host material soon inhibits the release of attractants. The attractiveness is highest during the initial phase of attack but then ceases as feeding gains momentum. However, Hunt *et al.* (1989) observed that α-pinene, a host terpene autoxidizes under normal temperature and atmospheric conditions to *trans*-verbenol, the aggregation pheromone produced by bark beetles. It then quickly further autoxidizes to verbenone, an anti-aggregation pheromone.

In the absence of semiochemicals newly emerged bark beetles fly downwind and once they encounter an attractive odour plume they fly upwind to the source (Safranyik *et al.,* 1989; Safranyik *et al.,* 1992). Newly emerged MPBs are also photopositive; they show preference for spot sources of light over diffuse light (Safranyik *et al.,* 1989). Despite this empirical evidence, mathematical models suggest that random host selection is sufficient for finding suitable hosts (Burnell, 1977; Byers, 1996). Other studies showed that landing rates were similar on host and non-host trees, suggesting that bark beetles disperse randomly within a stand and determine host suitability after landing (Hynum & Berryman, 1980; Moeck *et al.*, 1981; Raffa & Berryman, 1982a). Spatial analyses of attack patterns by Mitchell and Preisler (1991) indicated that trees were killed both randomly and selectively whilst Preisler (1993) later showed in another study that the probability of attack of a tree was greater than predicted by the random attack model.

The evidence concerning the expansion of infested spots in a stand is also inconclusive. Mitchell & Preisler (1991) observed that colonizing beetles fly to a new spot every year and do not expand or enlarge old spots. Borden (1993) found that some spots were abandoned by emerging beetles being displaced downwind whilst others were expanded by beetles from within the infested trees as well as aggregating beetles from outside the stand. Mark-recapture studies revealed that mean catches declined sharply with distance from the release point (Safranyik *et al.,* 1992). Only a small portion of the released beetles were recaptured, but of these, 86-93% were caught within 30 m of the release site. However, growth of a spot infestation and direction of spread depends on the number of flying beetles, the spatial and size distribution of trees and the speed and direction of wind (Safranyik *et al.*, 1989; Safranyik *et al.*, 1992).

The process of MPB aggregation is associated with a change in vigour class of infested trees. McCambridge (1967) showed that trees were infested at increasingly greater distances from the attractant center as beetle aggregation progressed. He also observed that proximity to infestation centres became more important for initiating infestation than tree diameter. Mitchell and Preisler (1991) also showed that the probability of attack increased with proximity to other infested trees. Their study also suggested that small trees are infested when beetle pressure is high simply due to their proximity to other infested trees but that they do not contribute to maintaining an outbreak. They attributed this phenomenon to host depletion, i.e. that large trees are attacked first and progressively smaller trees as fewer infested trees are available for infestation. Klein *et al.* (1978) observed that more small trees than large ones were killed, but larger trees were killed first at a rate disproportionate to their occurrence.

2.3. BEETLE-HOST INTERACTIONS

The MPB infest almost all pine species within its range (for details see Safranyik & Carroll, 2006). Coniferous trees are equipped with specialized secretory tissues which produce oleoresin, a mixture of monoterpenes and diterpene resin acids (Lewinson *et al.*, 1991). The resin accumulates in resin ducts, which are tube-like structures in the bark and wood of a coniferous tree. As beetles enter a tree they sever resin ducts causing constitutive resin to flow into the wound site, potentially flushing beetles back out of the entrance hole (Raffa & Berryman, 1982b, 1983a). This metabolically passive defence mechanism can delay beetle and fungus progress and inhibit pheromone emission by physically blocking the exit hole from beneath the bark such that the tree gains time to respond actively (Berryman, 1972; Raffa & Berryman, 1983a). Eggs completely covered by a thin layer of resin are killed entirely and mortality rate reduces to 40% when eggs are only half covered with resin. Embryos are not able to hatch through the hardened resin coating. The greater the amount of resin contact, the greater the mortality (Reid & Gates, 1970).

Trees also posses a secondary hypersensitive response that involves a quantitative and qualitative change in the monoterpene content of newly synthesized oleoresin (Reid *et al.*, 1967; Berryman, 1972; Shrimpton 1973; Raffa & Berryman, 1982b, 1983a). The result is that the beetle and its associated fungi are isolated in a lesion of dead cells. Resistant trees differ from susceptible ones mainly in their stronger response to invasion by the symbiotic fungi MPBs carry (Raffa & Berryman, 1982b). These aggressive fungi are lethal to newly attacked, vigorous trees (Safranyik *et al.*, 1975). *Ophiostoma clavigerum* and *O. montium* are the most virulent fungi associated with MPB (Shrimpton, 1978; Ayer *et al.*, 1986; Yamaoka *et al.*, 1990; Solheim, 1995). The beetles carry them in their maxillary mycangia and on their exoskeleton (Whitney & Farris, 1970; Six, 2003). The fungi kill trees by colonizing parenchyma cells in the xylem and phloem. The characteristic blue stain lags behind the leading edge of the fungal penetration (Solheim, 1995).

Given that the secondary response is energy demanding and requires translocation of phtosynthate, variation in host resistance is related to the overall vigour of the tree (Raffa & Berryman, 1982b). Resin flow increases with increasing diameter class and radial growth rate (Shrimpton, 1973; Safranyik *et al.,* 1974; Nebeker *et al.*, 1995). Outbreaks have been observed to coincide with declining radial growth (Shrimpton & Thomson, 1981, 1983). At the stand level, resistance is related to the incremental growth rate, in particular the current annual increment (CAI) and mean annual increment (MAI). Resistance to attack is greatest between 40-60 years when the current annual increment is at its maximum (Smithers, 1962). Resistance declines to low levels after about 80 years, which coincides with the intersection of MAI and CAI (Safranyik *et al.,* 1974; Shrimpton & Thomson, 1983). Aside from this general trend with increasing age, a tree's response fluctuates throughout the growing season (Reid & Shrimpton, 1971). Factors reducing tree vigour such as drought stress can be major factors contributing to outbreaks (Hopping & Mathers, 1945). The number of trees killed is therefore not only a function of the number of attacks but also of host susceptibility (Furniss & Schenk, 1969).

A tree's ability for secondary resinosis is limited such that the response to attacks diminishes with progression of beetle aggregation (Raffa & Berryman, 1983a). When MPBs aggregate, they can reduce resin flow by 65% within 2-3 days (Raffa & Berryman, 1983b). The success of attack is therefore determined by the interaction of the rate of the host's defence metabolism and the attack rate of the beetles (Raffa & Berryman, 1982b, 1983a,b). At a given level of resistance, the degree of host suitability for MPB reproduction is dependent on beetle density since a tree's vigour determines both the nutritional and resistance properties of the tree (Berryman, 1976; Raffa & Berryman, 1983b). To overcome the stronger defences associated with superior food sources, MPBs are thought to have evolved their semiochemical communication system, enabling coordinated mass-attacks (Berryman *et al.*, 1985; Sequeira *et al.*, 2000; Seybold *et al.*, 2000; Raffa, 2001). This dynamic relationship between vigour and beetle aggregation has implications on the spatial pattern of attack, which is the main subject of this thesis.

3. INTRODUCTION TO SPATIAL ECOLOGY

Ecologists analyse spatial patterns to infer underlying processes (Perry *et al.*, 2002). The premise is that ecological patterns and ecological processes are interrelated (Gustafson, 1998). However, the relationships between patterns and processes are often not unique; different mechanisms may lead to the same spatial pattern (Gustafson, 1998; Goreaud & Pélissier, 2003). Inference about mechanism from a pattern requires a careful, *a priori* statement of a theoretical relationship between an index and the ecological process (e.g. He & Duncan, 2000; Schurr *et al.*, 2004; Getzin *et al.*, accepted). Spatial randomness is used as a null model and implies the absence of mechanisms (e.g., competition, facilitation, predation, dispersal or reproduction) in pattern formation (Perry *et al.*, 2002). Even in the case where spatial pattern analysis may not help attribute a pattern to a particular process it can still be very useful for formulating testable hypotheses in manipulative studies.

The quantitative description of structure (or patches) and how patch characteristics vary in time and space is of central importance in ecology. One of the important applications of spatial pattern analysis is to identify appropriate scales at which mechanisms operate and to detect the spatial structure of a population (Gustafson, 1998). This information can aid management of patchy populations (Dalthorp *et al.*, 2000).

Knowledge of patch dynamics can provide insight into a species' ecology. Analyses of spatial pattern have been crucial to developing accurate predictive models in epidemiology and public health (Brownsetin *et al.*, 2003; Wu *et al.*, 2004; Griffith, 2005).

Spatial autocorrelation is the property of random variables such that values at sites close to each other are more similar than expected than for randomly associated pairs of observations (Legendre, 1993). Spatial dependence in data may cause variance inflation and hence incorrect confidence intervals (Dean, 1992; Legendre, 1993; Liebhold & Gurevitch, 2002). Almost all statistical techniques require the assumption of sample independence. Spatial autocorrelation clearly violates this assumption. Yet spatial correlation can be a nuisance as well as an opportunity (Legendre, 1993). The opportunity lies not only in the inference of an ecological mechanism for an observed spatial pattern, but the information about spatial correlation can also be used for spatial interpolation (Isaaks & Srivastava, 1989) or for reducing bias and increasing precision of model predictions (Keitt *et al.*, 2002). In regression analysis spatial autocorrelation can be incorporated as a predictor into autoregressive models (e.g. Griffith & Peres-Neto, *in press*). These models explicitly account for the effect of neighbouring sites and therefore provide more accurate results concerning the relative importance of explanatory variables (e.g. Gumpertz *et al.*, 1997; He *et al.*, 2003; Brownstein *et al.*, 2003; Keitt *et al.*, 2002).

Studies of spatial dynamics of bark beetles have served all of these motivations for spatial analysis of infestation. Økland and Bjørnstad (2003) identified synchrony in the spatial correlations of spruce bark beetle (*Ips typographus*) dynamics with environmental factors, revealing that windfall predisposes populations to outbreaks. Bark beetles also showed spatial association with windthrown spruces, resulting in a clustered pattern of infestation (Grodzki *et al.*, 2003). A variety of mechanisms may affect pattern formation at different scales. For example, Aukema *et al.* (2006) showed that the large-scale MPB infestation in BC likely originated in the west-central area of the province, then expanded eastward. Additionally, there were many localized eruptions in spatially disjunct locations that contributed to the large-scale outbreak. It was impossible to isolate the importance of dispersal amongst the subpopulations from an environmental factor such as temperature that may cause landscape-level synchrony of isolated populations. In another study, point pattern analysis revealed that patches of trees killed by Douglas fir beetle (*Dendroctonus pseudotsugae*) were clustered at a scale of 1 km and at 4 km (Powers *et al.*, 1999). Geostatistical analysis of the spatial association of pockets of high stem density and patches of trees infested by *D. pseudotsugae* suggested that management strategies could emulate the natural disturbance pattern of the beetle (Négron *et al.*, 2001). Gilbert *et al.* (2001) pointed out that a random pattern may occur if the scale of the study is too small relative to the dispersal range of the beetle.

The effective surveillance, management and control of a disease, pathogen or insect infestation require understanding its spatial spread and interaction with environment/host. Complications in the analysis of plant-pathogen interactions may arise from the fact that the plant population exhibits spatial structure over which a disease process is superimposed (Real & McElhany 1996). Campbell and Madden (1990) therefore discern between "true contagion" and "apparent contagion". True contagion is when an epidemic begins by infection of a few individuals. Due to the limited dispersal capabilities of the pathogen patches of high infection develop around plants initially infected. Apparent contagion is an aggregated pattern that arises from the spatial distribution of the host population with a pathogen that is dispersed randomly amongst susceptible plants.

4. RESEARCH OBJECTIVES

Despite the multitude of research efforts, no model has been developed that can estimate absolute, rather than relative risk of stands and provide reliable outbreak predictions (Bentz *et al.*, 1993; Shore *et al.*, 2000; Nelson *et al.*, submitted). Possible reasons include: 1) host susceptibility and beetle dynamics have mostly been studied separately and there is little information on how they interact; 2) the spatial structure of beetle population dynamics and dispersal, as well as stand conditions have not been sufficiently considered (Bentz *et al.*, 1993; Logan *et al.*, 1998); 3) differences in dynamics of endemic and epidemic population phases have been neglected (Bentz *et al.*, 1993); 4) there is a paucity of data for endemic population dynamics with low beetle density (Logan *et al.*, 1998); 5) controversy remains around dispersal mechanisms with a paucity of quantitative information on distance, spatial patterns and beetle density. I conducted two studies to address a part of these knowledge gaps. I was particularly interested in the effect of beetle population size on the spatial pattern of attack and the beetles' response to vigour.

Accurate data on attack occurrence and the pattern of infested trees is necessary for management of susceptible stands. Previous studies have shown that the probability of infestation of a tree increases with proximity to other infested trees (Mitchell & Preisler, 1991; Preisler & Mitchell, 1993; Preisler, 1993; Peltonen *et al.*, 2002). Yet there is little data characterizing the spatial pattern of attacked trees across scales under natural conditions. Inference of attack occurrence from data on beetle dispersal from mark-recapture studies where beetles were released from one point and captured with baited traps, is limited (Safranyik *et al.*, 1989, 1992). Given these gaps in knowledge the objectives addressed in Chapter 2 were to quantitatively describe the spatial pattern of attacked trees; to assess how, if at all, the spatial pattern of attacks changes with population size during outbreak progression; and to explore the relationship between host tree spatial patterning and that of attack. To achieve this, I tested the hypothesis of random dispersal amongst large diameter trees using innovative point pattern methods that account for the underlying host distribution.

The information on the scale of spatial autocorrelation from Chapter 2 aided developing a model in Chapter 3 for the probability of infestation as a function of host vigour (measured as DBH, tree height and crown length), local stand characteristics and infestation rate in the neighbourhood of a focal tree. I also wanted to assess how the relative importance of these factors changes with beetle population size over the course of an outbreak. Another objective was to determine how differences in stand conditions among plots affect the spatial pattern and the relative importance of factors for the probability of infestation. I used autologistic models to model the probability of infestation in the presence of spatial autocorrelation. The models were parameterized using a nonparametric jackknife estimation method. Results should be useful for developing a risk model for individual trees in high-value stands. I discussed implications for forest management and made recommendations for regulating beetle populations. An integrating discussion in Chapter 4 synthesized the results of Chapter 2 and 3.

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CHAPTER 2

SPATIAL ASSOCIATIONS OF TREES ATTACKED BY MOUNTAIN PINE BEETLES

1. INTRODUCTION

The development of effective risk models depends on knowledge of the spatial pattern and the scale at which infestation occurs. Spatially explicit models are invaluable tools in epidemiology and public health as they reduce bias and increase the precision of predictions (Brownstein *et al.*, 2003; Keitt *et al.*, 2002). Information on the spatial distribution of a pathogen is necessary to determine how far from a current outbreak a healthy individual needs to be for it to be safe, the spatial scale over which risk models should be developed, or the potential for different patterns associated with outbreak phase and stand conditions. Ecologists also study spatial patterns to infer underlying ecological processes (e.g. Perry *et al.*, 2002; Getzin *et al.*, in press). Studies of spatial dynamics of bark beetles have served all these purposes (Byers, 1992; Powers *et al.*, 1999; Gilbert *et al.*, 2001; Negrón *et al.*, 2001; Gilbert *et al.*, 2003; Grodzki *et al.*, 2003; Aukema *et al.*, 2006).

The mountain pine beetle, *Dendroctonus ponderosae* Hopk. (MPB), is a native bark beetle in Western North America. Recently the population in British Columbia has developed into a large-scale epidemic affecting 8.7 million hectares (Westfall, 2005). MPBs breed in most pine species but do so most commonly in mature lodgepole pine, *Pinus contorta* var. *latifolia* (Safranyik & Carroll, 2006). Controversy exists over the pattern of host selection by MPBs. Some suggest that they select hosts at random (Burnell, 1977; Hynum & Berrymen 1980), while others propose that beetles cue into host volatiles and selectively attack weakened trees (Gara *et al.,* 1984; Moeck & Simmons, 1991; Pureswaran & Borden, 2005; reviewed by Safranyik & Carroll, 2006) or orient towards large, dark silhouettes (Shepherd, 1966). After landing on the bark, beetles are thought to perform gustatory tests of its chemical constituents to determine the suitability of a potential host tree (Raffa & Berryman, 1982).

MPBs produce aggregation pheromones such as *trans*-verbenol once they commence feeding on host material (Pitman *et al.*, 1968). Responding to aggregation pheromones produced by pioneer beetles, a large number of beetles are attracted to a specific tree so that its defences are soon exhausted (Safranyik *et al.* 1973; Berryman 1976; Raffa and Berryman 1983; Berryman *et al.* 1989; Pureswaran *et al.* 2000). However, intraspecific competition for the limited phloem resource in a tree reduces reproductive success (Raffa & Berryman, 1983). In response to crowded conditions in the host tree, beetles produce anti-aggregation pheromones, such that newly arriving beetles "switch" from the focal tree to nearby trees (Geiszler *et al.*, 1980; Bentz *et al.*, 1996). Once the first tree has been infested within a stand, other trees nearby are infested within the next few days (McCambridge, 1967). These trees can become new sources of attraction, causing a chain reaction of attacks (Mitchell & Preisler, 1991). Geiszler and Gara (1978) also suggested that large plumes of aggregation pheromones may envelope nearby trees. Further aggregation mechanisms are discussed in greater detail by Safranyik and Carroll (2006).

These different mechanisms may act at different phases of the beetle population. My coworkers and I sought to describe how the spatial pattern of attack changes as an infestation progresses. If beetles attack hosts at random, we expected a random pattern of attacks amongst host trees (*Pinus contorta* var. *latifolia*). If, however, beetles respond to aggregation pheromones or plumes of host volatiles we expected the pattern to be more aggregated than a random distribution of attacked trees. We also expected that the zone of attraction surrounding an attacked host tree increases with attack rate. The size of clusters of attacked trees should increase with beetle population size. Cluster size may also be affected by the host distribution. As Real and McElhany (1996) point out, a disease may occur in clumps purely because of spatial aggregation of the underlying plant population. We expected attacked trees to be less aggregated when factoring out the host distribution than if we only analyzed the pattern of attacked trees without accounting for the host pattern. Since it is known that aggregation is mediated by pheromones the beetles produce in their hindguts (Pitman *et al.*, 1968; Vité and Pitman, 1968; Hughes, 1975), we expected the scale of aggregation to increase with population size.

In summary, the objectives of this study were: 1) to describe the spatial pattern of infested trees, 2) assess how, if at all, the spatial pattern of attacks changes with population size during outbreak progression, and 3) explore the relationship between host tree spatial patterning and that of attack.

2. METHODS

2.1 DATA COLLECTION

Together with my coworkers I established four study plots in the south western interior of British Columbia within an area that was subject to beetle activity (Figure 2-1 and 2-2). While A, B and H plots were located within 9 km of each other, E plot was approximately 313 km east and 24 km north of the other plots. All plots were located within unmanaged lodgepole pine dominated stands of similar age (90-119 years). E plot had the greatest stem density, followed by B and H plots (Table 2-1).

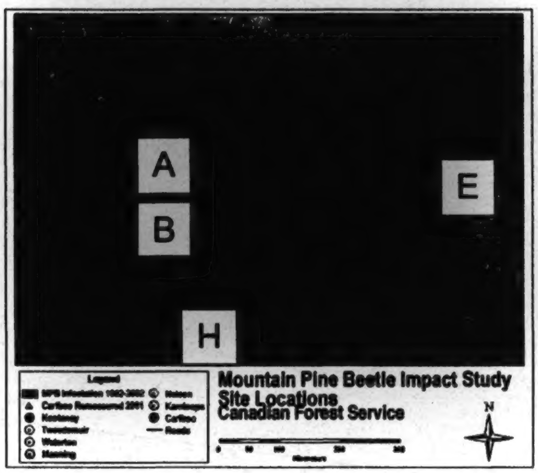

Figure 2-1 Locations of study sites in the southern interior of British Columbia

Table 2-1 Size, stem density and nearest neighbour distances of all plots. Density refers to all tree species with stems within the given DBH range. Nearest neighbour distance is the smallest distance between trees that are host species for the MPB and that have a minimum diameter of 8.2cm (the minimum diameter of infested trees).

Plots	**A plot**	**B plot**	**E plot**	**H plot**
Size	125x125 m	100×100 m	100×100 m	125×150 m
Density [stems/ha] DBH>8 cm	1685.02	1095	1840	941.87
Density [stems/ha] DBH>20 cm	512.38	573	611	395.20
Mean nearest neighbour distance [m] between pine trees with DBH≥8.2cm	1.45	1.89	1.64	1.95

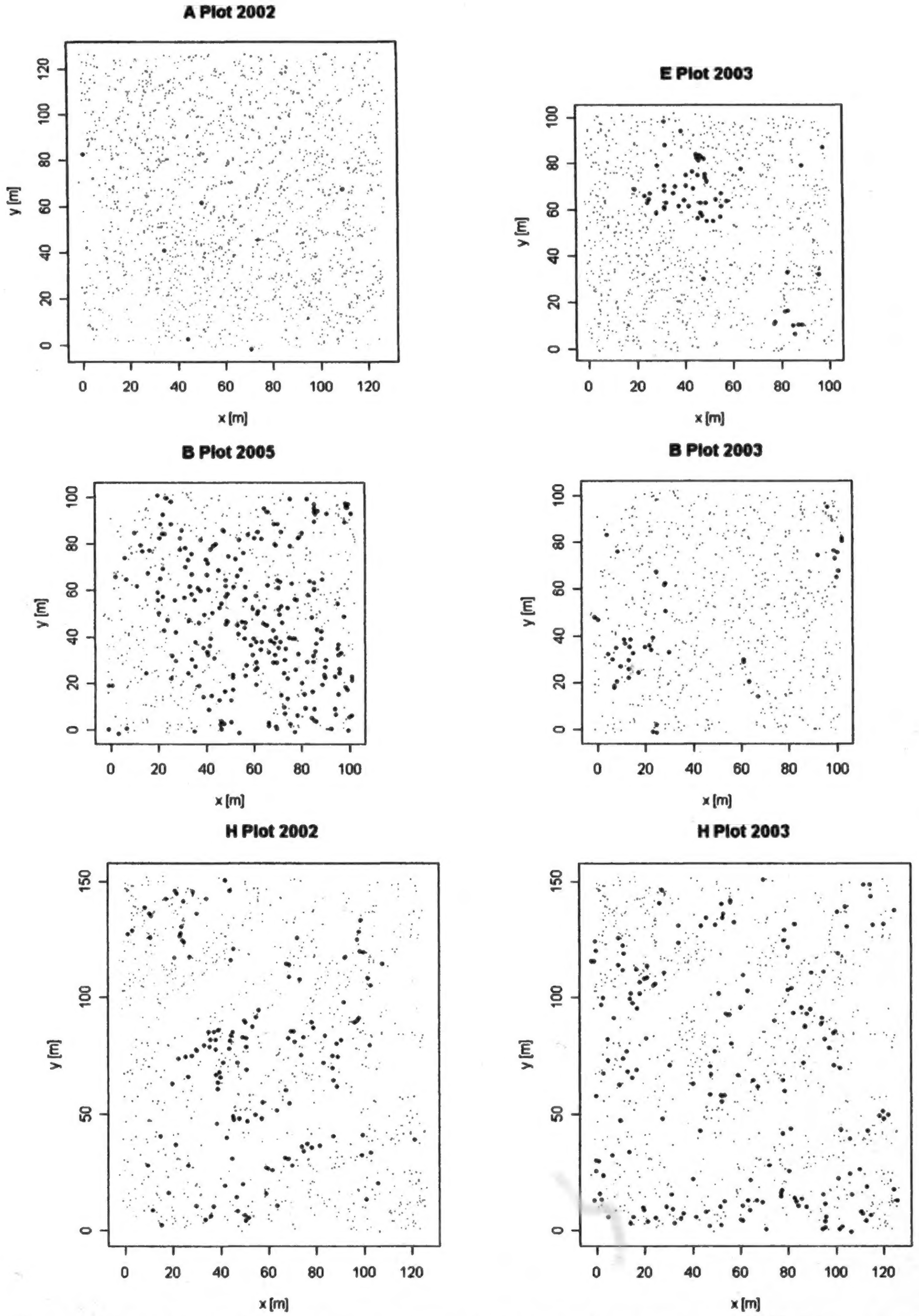

Figure 2-2 Maps of plots in Cartesian coordinates. Dots represent pine trees with DBH≥8.2cm; large black dots and small grey dots indicate attacked and unattacked trees, respectively.

Nearest neighbour distances between susceptible trees ranged from 0.10 m to 10.22 m with the means of plots ranging from of 1.45 m to 1.95 m (Table 2-1). Within these plots, all trees with a diameter at breast height (DBH) greater than 1 cm were mapped with a Nikon DTM-210 Total Station. MPBs typically do not attack trees with small DBH, since such trees do not have enough phloem to sustain a population (Amman, 1972; Cole, 1975 and other studies reviewed by Safranyik & Carroll, 2006). The minimum DBH of attacked trees observed in these plots was 8.2 cm; therefore our analysis only included lodgepole pines with DBH larger than 8 cm.

Table 2-2 Number of attacked trees per hectare for each year in each plot. NA indicates the plot was not surveyed that year. Since attacks can occur on the same tree in different years, the total number of trees attacked does not always equal the sum of attacks for all years. Only plots and years with at least 35 attacked trees per hectare were analyzed. These years are indicated in bold font.

	A plot	**B plot**	**E plot**	**H plot**
1999	0.00	2.00	NA	NA
2000	0.00	2.00	NA	NA
2001	1.81	4.00	6.00	10.02
2002	3.62	11.00	12.00	**77.49**
2003	7.85	**46.00**	**60.00**	**98.57**
2004	3.02	7.00	11.00	10.54
2005	1.81	**262.00**	NA	9.49
Total # trees attacked	30.00	325.00	80.00	206.10

With the exception of H plot, infestation data were collected in the area prior to stem-mapping. Each year, all trees were assessed for new attacks such that infestation data up to 5 consecutive years was available (Table 2-2). We mapped H plot when many trees had already been attacked; therefore, dates of attack were determined in retrospect by considering crown and wood condition, pitch tubes, galleries, boring dust and secondary bark beetles (for details see Safranyik & Carroll, 2006). All populations analyzed grew from incipient-epidemic populations and were analyzed in the epidemic phase. The beetle population in B plot was the largest of all plots in 2005 (Table 2-2). This heavy infestation was preceded by moderate infestation in 2003. In E plot the population gradually built up in 2001 and 2002 until it peaked in 2003. In relation to other plots, E plot had an intermediate level of infestation in 2003. The infestation in H plot was very heavy in 2002 and 2003 and declined in later years.

In A, B and E plots all attacks were recorded, including resisted and strip attacks (see Safranyik & Carroll, 2006). In contrast to the other plots, only successful mass-attacks were recorded in H plot. I included it in the analysis because the infestation was heavy and the number of partially attacked trees, (strip or resisted attacks) was likely small (Carroll A., unpublished data). The portion of trees colonized by MPBs with prior beetle attack declines exponentially with the number of attacking MPBs per hectare (Safranyik & Carroll, 2006). Since trees attacked by other beetle species can only subsequently be strip-attacked by MPBs, it is reasonable to assume that very few trees were partially attacked in the years analyzed here. For populations with 1000 beetles per hectare, the proportion of trees colonized by MPBs with prior beetle attack is approximately 5% (Safranyik & Carroll, 2006). Beetle population estimates for H plot far exceeded 1000 beetles per hectare in the year 2002 and 2003 (see Safranyik, 1988 for details on the method used to derive the population estimates).

2.2 STATISTICAL ANALYSIS

I used second-order point pattern statistics to analyse the spatial characteristics of attacked trees. While first-order point pattern statistics describe large-scale variation in the intensity of a point pattern, second-order point pattern statistics capture the correlation structure of a point pattern based on the distribution of distances of pairs of points (Ripley, 1981; Wiegand & Moloney, 2004). Second-order point pattern analysis has previously been used to aid the understanding of plant interactions (e.g. He & Duncan, 2000; Haase, 2001; Spooner *et al.*, 2004; Getzin *et al.*, in press) and for establishing reference conditions of old-growth stands for restoration efforts to maintain ecological integrity and forest health (Youngblood *et al.*, 2004). Since many ecological processes are scale dependent (Gustafson, 1998), an advantage of second-order statistics is that they describe a point pattern over a range of distances (Wiegand & Moloney, 2004), thus allowing the detection of different patterns across scales (e.g. Powers *et al.*, 1999). Point pattern analysis can also be used to account for natural variation in the background population (Bailey & Gatrell, 1995). This is of particular interest in epidemiological studies, because ignoring the host distribution will result in incorrect inference of dispersal mechanisms and make models untransferable to other host populations (Real & McElhany, 1996).

Both the *K*- and the *g*-function (pair-correlation function) were used here. To estimate the *K*-function, a circle of radius *r* is placed around each point (i.e. tree) and the number of points (except the focal point) covered by the circle is counted. The *K*-function therefore gives the expected number of points within distance *r* from an arbitrary point of the pattern divided by the intensity of the pattern λ (Ripley, 1981). $\lambda=n/A$ where *n* is the total number of points in the study region and *A* is the area of the plot. An edge corrected estimate is

$$\hat{K}(r)=\frac{1}{\lambda}\frac{1}{n}\sum_{i=1}^{n}\sum_{j=1}^{n}w_{ij}^{-1}I_r\left(\left|x_i-x_j\right|\right)=\frac{A}{n^2}\sum_{i=1}^{n}\sum_{j=1}^{n}w_{ij}^{-1}I_r\left(\left|x_i-x_j\right|\right),\quad j\neq i$$

where A is the area of the plot, n is the total number of points, x_i is the location of point i and x_j of point j, I_r is an indicator function that equals 1 when $|x_i - x_j| \leq r$ and zero otherwise and w_{ij} is a weighting factor correcting for edge effects. Usually a squared root transformation of the K-function ($\hat{L}$) is used for assessing deviation from the null model,

$$\hat{L}(r) = \sqrt{\frac{\hat{K}(r)}{\pi}} - r.$$

The L-function is zero under CSR such that $\hat{L}(r)>0$ indicates spatial aggregation, whereas $\hat{L}(r)<0$ indicates a pattern that is more regular than a random pattern.

An alternative approach, using rings or annuli instead of circles, is the pair-correlation function $g(r)$. This allows for isolation of specific distance classes, providing greater accuracy in defining the scale at which a pattern occurs (Wiegand & Moloney, 2004; Schurr *et al.*, 2004). While the K-function is based on the expected number of point pairs *within* a distance, the g-function is based on the expected number of point pairs *at* distance r from any arbitrary point of the pattern (Wiegand & Moloney, 2004). The g-function is a derivative of the K-function (Stoyan & Stoyan, 1994) because $K(r) = 2\pi \int_0^r g(t)t\,dt$, and the estimating function for g is

$$\hat{g}(r) = \frac{1}{2\pi r}\frac{A^2}{n^2}\sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}^{-1} k_h\left(r - |x_i - x_j|\right),$$

where k_h is an Epanečnikov kernel weighting point pairs within the ring according to their deviation from the exact distance r. When the distance between points differs from r more than h, the weight is zero. For all analyses conducted I used a ring width of 5 m to optimize the smoothness of $\hat{g}(r)$, given the nearest neighbour distances among susceptible trees (Table 2-1). $\hat{g}(r)>1$ indicates an aggregated pattern, whereas $\hat{g}(r)<1$ indicates a regular pattern. The analyses of L- and g-functions allowed me to determine which method is more useful in describing the patterns of MPB attacks.

The observed estimates $\hat{K}(r)$ or $\hat{g}(r)$ can be compared with those from various null models to determine departure from a random distribution. These include a homogeneous of a heterogeneous Poisson process, a Poisson cluster process and random labelling (Wiegand, 2004). Of these, the most common one is complete spatial randomness (CSR), implemented as a homogeneous Poisson process. The observed pattern of infested trees is compared to realizations of a simulated Poisson distribution. Under CSR, there are no interactions between the points of a pattern. However, random labelling is deemed more useful for examining the spread of a disease or pathogen (Goreaud & Pélissier, 2003; Wiegand, 2004). I used univariate random labelling to tests the hypothesis that attacked trees are a random subset of all trees. Under random labelling, attacked trees occur randomly within the spatial structure of all trees (Bailey & Gatrell, 1995). Since the two null models CSR and random labelling correspond to different confidence intervals, choosing an inappropriate null model can lead to incorrect biological conclusions. I wanted to investigate how results using the two null models differ and identify the conditions under which conclusions from an inappropriate null model will be incorrect.

Confidence envelopes were constructed with Monte Carlo simulations of realizations of the stochastic process underlying each null model (Bailey and Gatrell 1995). CSR was implemented as a homogeneous Poisson process. Thus, the probability of finding k points in an area W follows a Poisson distribution with mean λW, where the first-order intensity of the pattern λ is constant over the study region. When a pattern does not differ significantly from CSR, any point has an equal probability of occurring at any location in the study region such that the location of a point is independent of the locations of other points. Random labelling involves repeatedly assigning n_1 "case" labels (the number of attacked trees) to $n_1 + n_2$ trees (the number of attacked and unattacked trees), where each tree has equal probability of receiving a "case" label (Diggle, 1983). I assumed that the patterns of the attacked and unattacked trees were created by the same stochastic process and that the event of MPB attack affected the individuals of the single population *a posteriori*. Unattacked trees then act as a "control" pattern, a surrogate for environmental factors affecting the occurrence of all trees.

Each simulation using one of the null models generated an estimate $\hat{L}(r)$ or $\hat{g}(r)$. Confidence envelopes were calculated from the highest and lowest estimates of the function from n simulations of the null model. Ninety-nine simulations provide 99% confidence envelopes (Stoyan & Stoyan, 1994). If the function estimated from the actual data is outside the envelope it indicates departure from the null model. Significance was determined by comparing the estimates with Monte Carlo envelopes derived from the analysis of multiple simulations with randomly labelled points. I calculated both *L*- and *g*-functions using the *Programita* software (Wiegand & Moloney 2004). For each plot, the patterns of attack were analyzed separately in individual years if sample size was large enough (at least 35 attacked trees per hectare, Table 2-2). This enabled me to investigate changes in patterns over the course of outbreak progression.

I tested whether beetle population size increased the maximum scale of aggregation estimated by the *g*-function by conducting a linear regression analysis with

R. As surrogate for beetle population size I used the number of trees attacked by hectare. The confidence level was 95% ($\alpha = 0.05\%$).

3. RESULTS

3.1 COMPARISONS OF GLOBAL VS. LOCAL FUNCTIONS

Both $\hat{L}(r)$ and $\hat{g}(r)$ indicated spatial aggregation of attacked trees in all plots (Fig. 2-2 and Table 2-3). The two functions differed in the scale at which they indicate a significant departure from a random distribution of attacked trees. Whilst $\hat{L}(r)$ was greater than the upper confidence interval over all spatial scales analyzed in B plot in the year 2005, E plot in 2003 and H plot in 2002, $\hat{g}(r)$ showed a decline in aggregation with distance (Fig. 2-2 and Table 2-3). $\hat{g}(r)$ intercepted the confidence interval at different scales in each year and plot. Positive association of attacked trees in B plot 2003 was indicated by the *g*-function up to 16 m for both null models. In contrast to this, the *L*-function indicated aggregation up to 40 m under CSR and over all scales under random labelling. For the year 2003 in H plot, $\hat{g}(r)$ signified clumping from 3 to 10 m under random labelling, whilst $\hat{L}(r)$ showed a lagged response to changes in the spatial pattern, indicating clumping from 5-14 m.

The scale at which $\hat{g}(r)$ reaches its maximum can be interpreted as typical interplant distance (Stoyan & Stoyan 1994; Schurr *et al.*, 2004). In all cases, $\hat{g}(r)$ declined from the maximum value at the smallest distance from a focal tree to progressively smaller values as the distance increased (Figure 2-3). MPB's preferred to attack the immediate neighbours of a focal tree. As $\hat{g}(r)$ declined, the number of attacks at each distance class gradually approximated the number expected from CSR or random labelling. The maximum scale at which $\hat{g}(r)$ was significantly greater than the upper

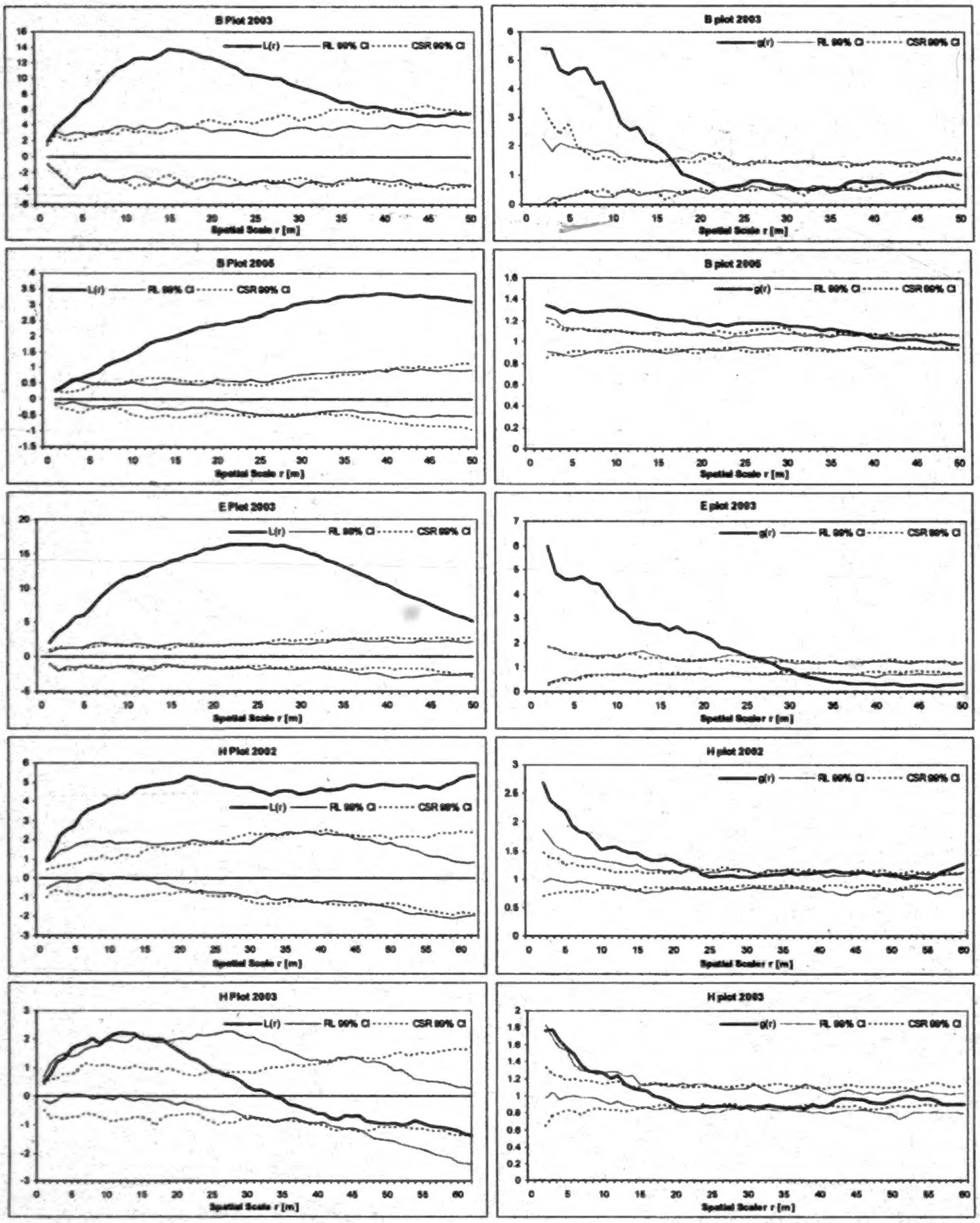

Figure 2-3 Results from $\hat{K}(r)$ and $\hat{g}(r)$ with random labelling and CSR confidence intervals. The squared root transformation of the *K*-function, $\hat{L}(r)$ is displayed since it is easier to interpret. Ninety-nine % confidence intervals for the random labelling null model are indicated by the solid grey line and the confidence bounds for the CSR null model are represented by the dotted line.

confidence bound can therefore be used to infer the size of attacked patches of forest. Within a patch, significantly more trees were attacked than would have been, had beetles attacked trees at random. Patch sizes ranged from 16 to 39 m (see Section 3.3 for a detailed discussion).

Table 2-3 Summary of results from the *K*- and *g*-functions with confidence bounds from CSR and random labelling null models. The *L*-function is the squared root transformation of the *K*-function. The spatial scale of aggregation indicates the range of distances for which the estimates are significantly greater than the expectation from the respective null model (see Figure 2-3). Due to sample size restrictions only years and plots with a minimum of 35 attacked trees per hectare were analyzed.

Plot	**Null model**	**Spatial scale of aggregation [m]**	
		***g*-Function**	***L*-Function**
B 2003	CSR	2-16	All scales
	Random labelling	2-16	All scales
B2005	CSR	2-39	All scales
	Random labelling	2-39	All scales
E 2003	CSR	2-27	All scales
	Random labelling	2-24	All scales
H 2002	CSR	2-23	All scales
	Random labelling	2-23	All scales
H 2003	CSR	2-13	1-25
	Random labelling	3-10	5-14, 16-18

There is no equivalent attribute of $\hat{L}(r)$ that could indicate typical interplant distance. $\hat{L}(r)$ peaked approximately at the same scale at which $\hat{g}(r)$ intercepted the upper confidence bound (Figure 2-3). Stoyan and Stoyan (1994) also suggested interpreting a maximum of $\hat{L}(r)$ as typical clump size, yet this is not always straightforward. A sharp peak in $\hat{L}(r)$ is easily identified at 15 m in B plot 2003 for example, yet in B plot 2005 $\hat{L}(r)$ declined gently so that a peak is not clearly identifiable upon visual assessment and would require more precise procedures (Figure 2-3). For H plot 2002 $\hat{L}(r)$ exhibited two maxima of similar magnitude at small and large scales. The corresponding *g*-function indicated highly significant departure from CSR and random labelling up to 23 m, and marginally significant departure from 38-51 m (40-44 m for CSR) and at spatial scales greater than 57 m. The initial decay in the relative frequency of interplant distances followed by a disjointed increase at larger scales suggests that the aggregated pattern at large scales did not arise from the same process determining aggregation at small scales. The aggregated pattern at large scales was most likely caused when the ring intercepted other patches. Such subtleties could not be inferred from the maxima of the *L*-function. Hence, the *g*-function provides more information on the characteristics of the spatial pattern of attacked trees than the *L*-function.

3.2 COMPARISONS OF NULL MODELS

Results from CSR were very similar to those from univariate random labelling, yet the CSR null model overestimated the scale of aggregation relative to random labelling in several cases. Differences appeared in the confidence intervals for 2003 in H plot where $\hat{g}(r)$ was within the random labelling confidence bounds up to 2 m and intercepted it again at 11 m. In contrast, $\hat{g}(r)$ estimates were consistently above the CSR upper confidence interval up to 13 m (Figure 2-3). Results from the *L*-function for the same plot and year showed an even larger discrepancy between the two null models. Whilst $\hat{L}(r)$ estimates did not significantly differ from random labelling of trees up to 4 m and attacked trees are positively associated up to only 18 m, the estimates were consistently greater than the CSR confidence intervals up to 25 m. This shows that with the same data, the overestimation of the scale of aggregation with CSR was greater for the *L*-function than the *g*-function. This is also supported by the fact that in B plot in

2003 $\hat{L}(r)$ intercepted the CSR upper confidence interval at 41 m but remained greater than the random labelling confidence interval over all scales (Figure 2-3). There was no discrepancy between null models with the *g*-function for the same data.

3.3 COMPARISONS AMONGST YEARS AND PLOTS

Typical patch size of attacked trees increased with attack rate in B plot from 2003 to 2005 (Table 2-2). The maximum scale of aggregation increased from 16 m in 2003 to 39 m in 2005. The respective increase in attack rate was from 46 to 262 attacked trees per hectare. In E plot only the year 2003 had enough attacks to analyze separately from other years. When compared with B plot in 2003 and 2005, the attack rate in E plot in 2003 was intermediate, with 60 attacked trees per hectare (Table 2-2). The maximum spatial scales of aggregation, 24 m for random labelling or 27 m for CSR, were also intermediate when compared to B plot (Table 2-2). H plot did not exhibit the same trend. Although the attack rate was higher than in E plot with 77.49 trees per hectare attacked in 2002, the

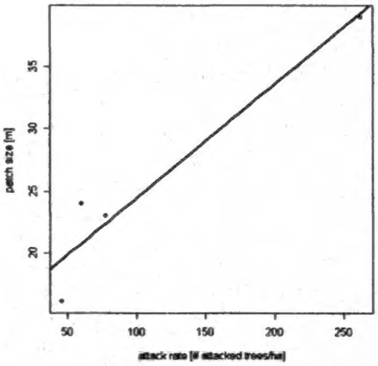

Figure 2-4 Patch size significantly increased with beetle population size. Attack rate (Table 2-2) served as surrogate for beetle population size. Data for H plot 2003 was not included in the linear regression analysis since host depletion may have altered the relationship in that plot. The line shows predictions of the linear regression model patch size = 15.299 + 0.091 x attack rate, where P=0.042 for the effect of attack rate on patch size and R^2=0.92.

maximum spatial scale of aggregation was only 23 m. H plot 2003 showed even greater deviation from a trend of increasing scale of aggregation with attack rate, since attacks were only spatially associated from 3 to 10 m, despite the rate of high attack (98.57 trees/ha). Even the *L*-function displayed a shorter scale of aggregation in 2003 in H plot to all other plots. Linear regression revealed that the number of attacked trees per hectare in the plots did not significantly increase patch size estimated by the *g*-function (P=0.121). However, when data for H plot 2003 was omitted, attack rate significantly increased patch size (P = 0.042, Figure 2-4).

4 DISCUSSION

4.1 COMPARISONS OF GLOBAL VS. LOCAL FUNCTIONS

The overestimation of the scale of aggregation by the *L*-function is an artefact of the "memory effect" that has been described for the *K*-function (e.g. Wiegand & Moloney, 2004). The mathematical proof of the "memory effect" can be found in Wiegand (2004, p.29). Since the *K* -function is accumulative, it conserves a "memory" of the small-scale pattern at subsequent larger scales. Larger circles include the same points as those of smaller circles such that the result is an average of both new and old information. Therefore, the cumulative *K*-function confounds effects at larger distances with effects at shorter distances (Penttinen *et al.* 1992). This makes the *K*-function less sensitive to changes in the pattern with distance, as the lagged response in $\hat{L}(r)$ to the change from an aggregated to a random pattern in H plot 2003 shows. I conclude that the

K-function may be useful for identifying typical patch size when considering only the scale at which the estimates reach their maximum value. Results for scales greater than the scale at which the estimates reach their first peak are distorted by the "memory effect". For information on typical interplant distance and a trend on the frequency of point-pairs relative to the null model, the *g*-function was more useful.

4.2 COMPARISON OF NULL MODELS

The overestimation of aggregation under the CSR null model relative to the random labelling null model is due to "virtual aggregation" (Wiegand, 2004). The overestimation arose from the violation of the assumptions of the homogeneous Poisson process used for generating CSR confidence intervals. If the spatial pattern of hosts is not homogeneous (i.e. the first-order intensity λ of trees is not constant for the entire study area) the null model of CSR is not suitable for analyzing second-order effects (Wiegand, 2004). Trees in H plot, for example, were not distributed homogeneously (Figure 2-2). A swamp in the centre of the plot and ridges of two steep hills created conditions unfavourable for tree survival. Ridges of steep hills can be rocky and very dry as water runs down the steep slopes. In this case, the observed departure from CSR mainly reflects large-scale first order effects rather than fine-scale second order effects (Bailey & Gatrell, 1995). The bias was more severe with the *K*-function than the *g*-function, as it accumulates with increasing radius size.

If there are areas in a stand where conditions are unsuitable for host trees to survive, it violates the assumption that all locations have equal probability of being attacked. When the local density of host trees exceeds average density of the entire plot there will also be more attacked trees in the close neighbourhood of other attacked trees than expected under homogeneity, even if attacked trees are distributed randomly amongst host trees. The homogeneous Poisson model created confidence intervals that are incorrect for the hypothesis that beetles attack trees at random. A null model that is more appropriate than CSR for analyzing the distribution of attacked trees in space is a heterogeneous Poisson process. For simplicity and comparability of the different plots I only used CSR. Given that it is the most widely used null model, I also wanted to determine under which circumstances it is not appropriate to use CSR.

Since random labelling distributes "attack" labels amongst locations of host trees, it has the advantage of making no assumptions of homogeneity. It accounts for large-scale environmental heterogeneity by using the pattern of host trees as a "control" pattern (Wiegand, 2004). This also makes it possible to compare results from different sites. It is also more appropriate for analyzing host selection behaviour of the beetle, a truly second-order effect imposed *a posteriori* onto the pattern of hosts that was subject to first-order effects prior to infestation. Where results from CSR differed only slightly from random labelling the host pattern was most likely not very different from random, such that it did not severely influence the pattern of infestation, except in H plot.

4.3 COMPARISONS AMONGST YEARS AND PLOTS

The aggregated pattern of attacked trees can be explained by the pheromone coordinated attack strategy MPBs employ. Epidemic MPBs preferentially attack large-diameter trees within a stand (see Safranyik & Carroll, 2006). Although large trees have stronger defences than do small trees, the symbiosis with lethal fungi and the pheromone mediated mass attacks allow beetles to successfully colonize large trees when population densities are high (for a detailed discussion of the interactions between fungi, MPBs and tree defences see Safranyik & Carroll, 2006). Beetles emit aggregation pheromones to attract a large number of beetles to the tree so that its defences are soon exhausted (Safranyik *et al.* 1973; Berryman 1976; Raffa and Berryman 1983; Berryman *et al.* 1989; Pureswaran *et al.* 2000). Once the first tree has been mass-attacked within a stand, other trees nearby are attacked within the next few days (McCambridge, 1967; Geiszler *et al.*, 1980). This may give rise to the aggregated pattern of attack in the landscape (Mitchell & Preisler, 1991; Preisler & Mitchell, 1993; Preisler, 1993).

The discrepancy between the observed number of attacked trees and the number expected from a random distribution was highest in the immediate vicinity of another attacked tree and declined with distance. This suggests that beetles preferentially attack trees in close vicinity of focal trees over trees further away. The spatial decline of the greater attack frequency relative to a random distribution could reflect a diffusion process of pheromones from an infested focal tree. Geiszler and Gara (1978) suggested that pheromones produced in an infested tree envelope trees nearby such that these are attacked as well. Bentz *et al.* (1996) found that neighbouring trees were infested prior to the total infestation of a focal tree and concluded that there is a cumulative effect of all trees in the vicinity that are under attack. If beetles attack trees according to pheromone concentrations enveloping a tree, more beetles would attack trees close to the pheromone source than trees with smaller ambient pheromone concentrations.

In addition, beetles produce anti-aggregation pheromones to avoid crowding within a tree, such that newly arriving beetles "switch" from the focal tree to nearby trees as beetles approach optimal colonization density (Geiszler *et al.,* 1980). Above 62 females/m^2 bark larval and pupal productivity declines due to intraspecific interference and scramble competition (Raffa & Berryman, 1983). The effect of anti-aggregation pheromones are thought to occur over small distances (e.g., Ryker and Yandell 1983; Borden *et al.* 1987). Beetles that locate the source of an attractive odour plume are repelled from the focal tree by anti-aggregation pheromones and disperse to neighbouring trees. Mark-recapture studies showed that a small proportion of the released beetles engaged in short range dispersal and that up to 93 % of the recaptured beetles did not fly further than 30 m from the release point (Safranyik *et al.*, 1992). The number of beetles decreased exponentially with distance which could be reflected in the decreasing number of attacked trees with distance, relative to randomly attacked trees. However, multiple other mechanisms for beetle aggregation and the action of pheromones have been suggested (see Safranyik & Carroll, 2006).

We did not analyze the spatial pattern of landings on individual trees. The results of this study provide insight into the process of attempted gallery construction, regardless of its outcome. Hynum and Berryman (1980) suggested that landing and attack (i.e. gallery initiation) are two separate processes. Pioneer beetles appear to land at random, unable to distinguish between tree species and whether the tree is dead or alive whilst in flight (Hynum & Berryman, 1980; Pureswaran & Borden, 2005). By contrast, other studies suggest that beetles respond to host volatiles indicative of its vigour state (Gara *et al.,* 1984). However, MPBs landed equally often on lodgepole pine and Douglas fir trees baited with synthetic pheromones, suggesting that beetles respond more strongly to pheromones than host odours that would possibly allow discrimination of host from non-host species (Pureswaran & Borden, 2003). This suggests that host volatiles may be important only during the pre-aggregation phase in the absence of pheromones (Pureswaran & Borden, 2005). MPBs only produce pheromones after they have penetrated the bark (Pitman *et al.*, 1968). Thus, prior to the first attack beetles cannot orient in a stand by responding to pheromones.

There is little information on the dispersal behaviour of MPBs during the pre-aggregation phase, possibly because most statistical tests require a large sample size. A rule of thumb for second-order point pattern analysis is a minimum of 35-40 cases per hectare (Getzin, *personal communication*). For this reason we could not analyze A plot quantitatively (see Table 2-2). In 2002 all attacks were strip attacks, suggesting that the quantity of pheromones in the plot was most likely very low, approximating a pre-aggregation situation. Visual comparison of the spatial pattern of attacks in A plot with other plots showed that typical distances between attacked trees were much larger than in other plots (see Figure 2-2). Mean minimum distance amongst attacked trees in A plot 2002 was 36.58 m compared to 2.78 m in B plot 2005. When pheromones are absent or present only at very low concentration, MPBs did not focus their attacks on one tree sufficiently to kill it. Instead, they partially attacked several trees far apart from each other.

In conjunction with the observation that patch size increases with population size, the lack of aggregation in the endemic phase supports the hypothesis that aggregation is a process initiated by beetles and not by tree characteristics. The most likely process is the "self-focusing" mechanism of conspecific attraction (White & Powell, 1997). Host volatiles do not seem to cause spatial associations of attacked trees, even in the pre-aggregation phase. These results do not provide evidence for random landings in the endemic situation, as we cannot rule out the possibility that beetles respond to factors that act at spatial scales too small to affect the attack probability of neighbouring trees.

The spatial scale of aggregation is not determined by the beetle population size alone. After a high rate of infestation in 2002, the scale of aggregation in H plot declined in 2003 despite an increase in the beetle population. This was most likely due to host depletion. When considering the distribution of attacked trees within the spatial pattern of host trees (i.e. random labelling null model), there was also no significant spatial association of attacked trees at distance classes smaller than 3 m in 2003. Conversely, the typical distance between attacked trees in 2002 was the minimum distance between susceptible trees. Given that the relative frequency of attacks declined with distance from a focal tree, the depletion rate of the host resource will be greatest in the centre of a patch, i.e. at small spatial scales.

The patches of forest infested in 2002 turned into patches of low density of available host trees in 2003. Trees infested in 2002 were not included in the analysis for 2003. The spatial distribution of large living lodgepole pine trees was more patchy in 2003 than in 2002, which is reflected in the greater severity of "virtual aggregation" in 2003 (Section 4.2). Beetles had to locate the remaining live trees interspersed among dead trees. If beetles cannot discern between dead and alive trees while flying, as Hynum and Berryman (1980) suggest, beetles attacking in 2003 will land more frequently on dead trees than beetles attacking in 2002. An increased number of landings and subsequent take-offs may disorient beetles. The greater difficulty for beetles to locate suitable hosts in a more heterogeneous stand may inhibit their ability to focus attacks.

The fact that H plot showed smaller scales of aggregation than other plots before the host resource was severely depleted may be the result of stand conditions not accounted for by the random labelling null model. Inconsistencies with other plots may have arisen if pheromones are dispersed differently in H plot. Stem density in H plot was lowest of all plots (Table 2-1) which may have affected its microclimate. Within spaced stands solar radiation is greater than in dense stands and wind speed and air turbulence are also higher (Whitehead *et al.*, 2004). Since pheromones are airborne substances, they are easily dispersed by wind, as are flying MPBs. Mark-recapture studies revealed that wind and temperature strongly affect the beetle's flight direction (Safranyik *et al.*, 1989; Safranyik *et al.*, 1992). In an open stand pheromones may be more diluted or beetles may disperse differently than in denser stands where wind speed will be reduced.

5. CONCLUSIONS

1) Attacked trees occurred in an aggregated fashion within a stand up to a distance of 39 m. The larger observed number of attacked trees relative to a random distribution was highest in the immediate neighbourhood of a focal tree and decreased with distance. I suggest further research to establish a causal relationship between pheromone diffusion from attacked trees and the observed decline in the relative frequency of attacked neighbours with increasing distance from an attacked focal tree.

2) Patch size increased with population size. However, in years after a high rate of infestation, the distance between attacked trees increased and patch size declined. At very low population density when conspecific attraction was weak, distances between attacked trees were very large.

3) Results from the null model of complete spatial randomness (CSR) did not differ much from random labelling when the underlying host distribution did not show a strong spatial pattern. Where the host distribution was patchy, CSR overestimated the scale of aggregation. The random labelling null model is more appropriate than CSR for studies aiming at investigating disease spread and comparing results between different study regions. Microclimate may also affect the spread of pheromones and beetles, resulting in smaller patches in stands of lower density. The implication for aerial surveys of MPB infestation is that population estimates based entirely on the size of infested patches may not be accurate.

4) The *K*-function consistently overestimated the scale of aggregation. The overestimation can be attributed to the "memory effect". Nevertheless, the first maximum of the *K*-function can be useful for inferring the typical size of infested patches. We suggest that analyses of spatial patterns would greatly benefit from local measures such as the *g*-function, as they provide valuable information about changes in a spatial pattern at specific scales.

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CHAPTER 3

MOUNTAIN PINE BEETLE INFESTATION RISK: A FUNCTION OF HOST VIGOUR AND BEETLE AGGREGATION

1. INTRODUCTION

Much is known about how mountain pine beetles (MPBs) infest trees but the details of host selection remain unclear (Safranyik & Carroll, 2006). Some studies indicate that beetles land on trees at random (Burnell, 1977; Hynum & Berryman, 1980; Mitchell & Preisler, 1991), while others show that the beetles respond to visual and gustatory cues or to volatiles produced by fungal decay of host constituents (Shepherd, 1966; Raffa & Berryman, 1982a; but see Pureswaran & Borden, 2005). The dominant theory proposes that beetles respond to a combination of these stimuli (see Safranyik & Carroll, 2006). If beetles respond to host cues, pioneer beetles will attack trees with weakened defences before the population aggregates in response to pheromones. Selection behaviour may change with increasing beetle population size. If more beetles aggregate than are necessary for killing trees of low vigour, infestation may not be restricted to weak trees. My coworkers and I tested the hypothesis that tree vigour, local stand characteristics and the infestation status of neighbouring trees affect the risk of infestation, and that the relative importance of these effects changes with MPB population size. The aim of this study was to model the MPB infestation rate and identify tree attributes and stand characteristics that affect it. The approach taken here differs from previous work (Mitchell & Preisler, 1991; Preisler, 1993; Preisler & Mitchell, 1993; Gumpertz *et al.*, 2000) in that my coworkers and I were able to examine the relative importance of these factors at different population phases.

1.1 TREE VIGOUR AND HOST SUSCEPTIBILITY

The growth-differentiation balance hypothesis, the plant-stress hypothesis and various other plant defence hypotheses suggest that since growth processes and differentiation of plant cells utilize the same metabolic precursors, there is a trade-off between growth, maintenance, storage, reproduction and defence (Loomis, 1932; Waring & Pitman 1983; Lorio, 1986; Herms & Mattson, 1992; Stamp, 2003). Given the life-history traits of coniferous trees that are long-lived with low metabolic rates, stress tolerance is more important for maximizing fitness than is growth rate (Grime, 1977). With a long exposure to herbivores and a poor ability to compensate for tissues lost by herbivory, trees have developed elaborate defence mechanisms to minimize herbivory (Lewinson *et al.*, 1991; Paine & Hanlon, 1994; Klepzig *et al.*, 1996; Fransceschi *et al.*, 2005).

Lodgepole pine trees respond to attack by MPBs by flushing beetles out of the wound site with constitutive resin. There is also a secondary hypersensitive response to inoculation with fungi associated with the beetles (reviewed by Safranyik & Carroll, 2006). It involves quantitative and qualitative changes in the chemical composition of newly synthesized and translocated oleoresin causing a lesion of dead cells. Resistant trees secrete a greater amount of monoterpenes around the inoculation site than do susceptible trees (Raffa & Berryman, 1982b). The production of such complex compounds is energy demanding and requires the translocation of photosynthates (Waring *et al.*, 1980; Christiansen & Ericsson, 1986; Kozlowski, 1992).

For this reason the growth-differentiation balance hypothesis predicts that growth takes precedence over differentiation when resources are abundant. When resources are moderately limited plant growth may be more restricted than photosynthesis (see Hermes & Mattson, 1992). In such environments the diversion of excess photosynthates from primary metabolism (growth) to secondary metabolism (e.g. the synthesis of complex defence chemicals) prevents the build-up of metabolites and the subsequent negative feed-back on photosynthesis. The exception to this prediction is when the limiting factor is light, resulting in equal restrictions in growth and photosynthesis (Lerdau *et al.*, 1994; Stamp, 2003). Competition for light may be severe in mature forest stands and drought stress is also prevalent in the dry interior Douglas-fir biogeoclimatic zone of British Columbia where the sites analyzed in this study are located (Lloyd *et al.*, 1990). In resource poor environments the growth-differentiation hypothesis may provide the same prediction as the plant-stress hypothesis, i.e. that growth and resistance are positively correlated (Waring & Pitman, 1983, 1985; Lerdau, 1992; Stamp, 2003).

There is ample empirical evidence for this prediction from bark beetle studies, including the positive associations between resistance to MPB infestation and the current annual increment (Shrimpton, 1973; Safranyik *et al.,* 1974; Shrimpton & Thomson, 1983), between resin flow and diameter class (Safranyik *et al.,* 1974; Nebeker *et al.*, 1995) and between inducible defences and growth (Lobardero *et al.,* 2000; Bleiker *et al.*, 2005). This implies that trees with superior nutritional qualities for MPB reproduction are also the ones with the strongest defences. Reproductive success (Reid, 1963; Amman, 1972; Cole, 1975; Berryman, 1976; Waring & Pitman, 1983) as well as resin flow (Shrimpton, 1973; Safranyik *et al.,* 1974; Nebeker *et al.,* 1995) increase with tree diameter and phloem thickness. This apparent paradox (Berryman, 1976, 1982) results in a threshold relationship between tree vigour and the number of beetles required for successful attack (Berryman 1972; Waring & Pitman, 1980; Raffa & Berryman, 1983a). I therefore expect that the effect of vigour covariates (DBH, height, crown length) on the probability of infestation changes with population size. When the population is small, there are too few beetles in the stand to attack and overcome defences of very vigorous trees and weak trees will be preferred. At large population sizes, host vigour constrains beetles less and they may exhibit a preference of more vigorous, more nutritious trees (see Safranyik & Carroll, 2006).

1.1.1 MEASURES OF VIGOUR

Often it is impossible to measure vigour directly for thousands of trees. Therefore, we assessed the effects of tree height, crown length and diameter at 1.3 m (DBH, i.e. diameter at breast height) on susceptibility to infestation. Due to competition for light, carbon is first allocated to vertical growth and the excess is stored in the bole (Waring & Pitman, 1985). Trees with large DBH will, therefore, have more carbon available for defence than a slender tree. DBH is also a measure of phloem thickness, the primary food source for MPBs. Thicker phloem leads to greater reproductive success of beetles (Amman, 1972; Cole, 1975; Waring & Pitman, 1983). Trees with small diameters have too thin phloem to sustain a large population (Berryman, 1976).

Tall trees usually dominate the canopy of a stand, capturing more light than shorter trees. While tall trees have more resources available for the production of defensive compounds, they may also be more nutritious for MPBs. Both height and DBH reflect the crucial characteristics of the beetles' food source, so we expect their effects to be consistently positive, although their importance may be reduced for small populations. Reduced photosynthetic capacity may affect the tree's ability to produce defensive chemicals. In particular, defoliation has been suggested to increase susceptibility to bark beetles or their symbionts (Miller & Berryman, 1986). There is also evidence that the number of attacking beetles and brood production is greater for trees with large crowns (Safranyik, 1968; Safranyik & Carroll, 2006). Small populations are severely affected by tree vigour, as the tree has time to synthesize new toxic resin whereas when attack rate is very high the tree is quickly overcome (Raffa & Berryman, 1983a). The beetle population will experience higher mortality from strong defences in vigorous trees when it is small than when it is large. Hence, I expect crown length to have a negative effect on small populations and a positive effect on epidemic populations.

1.1.2 STAND CONDITIONS AFFECTING VIGOUR

Reducing stand density has been used to reduce infestation rates (Whitehead & Russo, 2005). Trees in dense stands experience greater competition for resources and therefore have low vigour and thin phloem. Attack rate is highest at intermediate stand density from 750 to 1500 stems per hectare (Anhold & Jenkins, 1987; Shore & Safranyik, 1992). Since the plots used in this study are in the lower range of that stand density spectrum deemed to be susceptible (Table 3-2), the infestation risk to a tree is expected to increase with stem density within its neighbourhood. Infestation of such trees would likely occur only when the beetle population is small and restricted to weak trees. When the population is large, beetles may prefer more nutritious trees that have a greater quantity of resources. Larger trees will exert greater competitive pressure, such that trees surrounded by many large trees are expected to have low defensive capacities. Basal area reflects the sizes of all neighbours and hence the degree of competition faced by a tree.

Resource availability in the abiotic environment also influences vigour. Water may limit growth in these study plots, since they are situated in a biogeoclimatic zone which is characterized by a shortage of moisture during the entire growing season (Lloyd *et al.,* 1990). Trees on hills or steep slopes may further increase susceptibility for the same reasons. My coworkers and I therefore expect that elevation and slope have a positive effect on the risk of infestation in years of low infestation rate. Greater solar energy interception increases sapwood width and radial growth rate (Yang & Murchison, 1992). Assuming that trees with southern aspects are more vigorous than those with northern aspects, trees on south facing slopes will be less susceptible to small beetle populations. I expect that abiotic effects will not be of significant importance when a very large beetle population is present. When the beetle population is small host vigour is more deleterious than when there is a very large epidemic and the attack rate is high and trees are quickly overcome (for details see Raffa & Berryman, 1983b and Safranyik & Carroll, 2006). Abiotic factors may have more subtle effects that direct measures of tree size.

1.2 MPB AGGREGATION

MPB infestation is a contagious process. Spatial aggregation of MPB attacks is the manifestation of a "switching behaviour" from focal trees to nearby trees (McCambridge, 1967; Geiszler *et al.*, 1980; Mitchell & Preisler, 1991; Preisler & Mitchell, 1993). These self-focussing and self-dissipating forces create a non-linear density dependent response (White & Powell, 1997). The resultant variation in the probability of infestation cannot be explained by tree characteristics alone. Infestation rate is expected to increase with increasing infestation of neighbouring trees.

The aggregation behaviour of MPBs gives rise to autocorrelation, thus, observations are not independent. Failing to account for spatial dependence may result in over- or under-estimation of the relative importance of explanatory variables, which may lead to inaccurate conclusions concerning the underlying ecological mechanisms involved (Keitt *et al.*, 2002; Brownstein *et al.*, 2003; Lichstein *et al.*, 2002). Previous stand-level studies of MPB attacks have used Markov Chain Monte Carlo (MCMC) methods to parameterize autologistic models (Mitchell & Preisler, 1991; Preisler & Mitchell, 1993; Preisler, 1993). However, implementing MCMC methods is not always straight forward and as Lichstein and others (2002) have pointed out, there is a need for readily available software for implementing spatial models in ecology. Hence, a secondary objective of this study is to demonstrate the use of a nonparametric Jackknife for estimating accurate standard errors (Lele, 1991).

2. METHODS

2.1 THE DATA SET

MPBs commonly attack mature, moderately dense, lodgepole pine (*Pinus contorta* var. *latifolia*) stands (Shore *et al.*, 2000). Six study plots were set up in the south-western interior of British Columbia where beetle activity was occurring (Figure 3-1). A, G, E and B plot were set up in 2003, F plot in 2004 and H plot in 2005. A detailed stem-mapping technique was used to create maps with spatial coordinates of all trees with a minimum DBH of 1 cm. My coworkers and I used a Nikon DTM-210 Total Station to record the spatial coordinates and elevation of each tree. DBH was measured for every tree with a calliper and height for trees with an intact terminal using a hypsometer. Crown length was calculated as the difference between tree height and the height of lowest live branch. All plots studied here were established in unmanaged, lodgepole pine dominated stands. The plots were all square or rectangular in shape, ranging from 1.00 to 2.25 ha in size (Table 3-1). Table 3-1 shows that H plot has

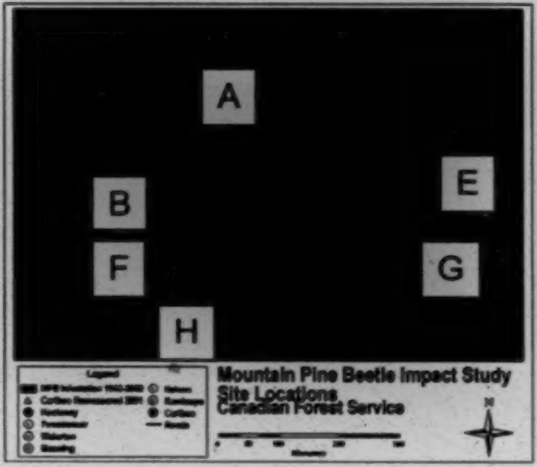


Figure 3-1 Locations of study sites in the southern interior of British Columbia

the lowest basal area, whereas B plot, A plot, E and F plot had similar basal areas; G plot has the greatest basal area. The density of trees of all species with a minimum DBH of 1 cm was lowest in B plot (Table 3-1), followed by H plot, A, B and G plots with intermediate densities and F plot exhibited the highest density.

Table 3-1 Plot characteristics including plot dimensions, age and measures of forest structure. Basal area includes living trees of all species with a minimum DBH of 1cm. Density refers to the density of living trees of all species.

	A plot	B plot	E plot	F plot	G plot	H plot
Size [m]	125x125	100x100	100x100	125x125	150x150	125x150
Age [years]	109.48	116.54	90.71	119.49	108.63	119.00
Basal area [m^2/ ha]	46.88	40.49	50.69	50.25	56.97	32.72
Density of trees with DBH>1cm [stems/ ha]	2442.24	1365.00	2327.00	3662.72	2428.89	1733.87
Density of trees with HT< 10m [stems/ ha]	911.71	357.00	679.00	1991.04	489.33	947.20

With the exception of H plot, infestation data were collected in the area prior to plot mapping. Each year all trees were assessed for new infestations, such that infestation data up to 5 consecutive years was available (Table 3-2). H plot was mapped when many trees had already been infested, several of which were already dead. Dates of infestation for trees in this plot were determined retrospectively by considering crown and wood condition, pitch tubes, galleries, boring dust and secondary bark beetles (For details see Safranyik & Carroll, 2006). Only successful mass attacks were analyzed. According to the population phases outlined in Safranyik and Carroll (2006), A, F and G plot remained in the incipient-epidemic phase, whereas the populations in B, E and H plot transcended the incipient-epidemic threshold (Table 3-2). Later years in H plot represented post-epidemic conditions.

Table 3-2 Density of mass attacked trees for each year in each plot. NA indicates that the plot was not surveyed that year. Empty cells had too few infested trees to analyze.

	A plot	B plot	E plot	F plot	G plot	H plot
2001	0.00	0.00	0.00	0.00	0.00	10.93
2002	0.00	0.00	7.75	0.00	0.44	75.48
2003	4.34	24.87	37.77	1.26	1.31	97.35
2004	0.62	6.7	10.65	3.14	0.87	10.41
2005	1.86	216.44	NA	13.19	0.00	8.85

2.2 STATISTICAL ANALYSIS

2.2.1 THE MODEL

The probability of infestation for a tree was modeled as an autologistic model to incorporate the neighbourhood effect caused by spatial correlation of MPB attacks. Observed responses $Y_i\ (i=1,\ldots,n)$ had the value 1 if the i^{th} tree was infested and 0 if it was not infested. For logistic regression, the probability of infestation $\pi_i = P(Y_i = 1)$ is assumed to follow a binomial distribution with a logit link function, such that $\pi(X) = \frac{e^{(X\beta)}}{1+e^{(X\beta)}}$. Since this is difficult to estimate, usually log π is evaluated. The "log odds ratio" $\log\left(\frac{\pi}{1-\pi}\right) = X\beta$ gives the odds of Y=1 for a given value of X (Ryan, 1997).

Autologistic regression is a special case of a logistic regression model where the response at location i is a function of the responses at other locations. They are included in the regression model along with other potential explanatory variables (Augustin *et al.*, 1998). Covariates of neighbouring responses were calculated for concentric circles of 5 m intervals up to 25 m distance from a focal tree. Thus, I was able to determine the maximum distance within which spatial dependence of infestation was significant. The infestation rate in the neighbourhood was calculated for each focal tree, along with stem density, basal area and density of susceptible trees. To correct for edge effects, trees within 15-25 m from the edge of the plots only served as neighbours, not as focal trees. The breadth of the boundary was chosen such that a sufficient amount of infested trees remained for the analysis.

The full model comprises measures of growth for each tree as well as the explanatory variables calculated for the circles:

$$\begin{aligned}\log\left(\frac{\pi_i}{1-\pi_i}\right) = {} & \beta_0 + \beta_1 elevation_i + \beta_2 slope_i + \beta_3 aspect_i + \beta_4 DBH_i + \beta_5 HT_i + \beta_6 CL_i + \\ & \beta_7 IP_{5m_i} + \beta_8 IP_{10m_i} + \beta_9 IP_{15m_i} + \beta_{10} IP_{20m_i} + \beta_{11} IP_{25m_i} + \\ & \beta_{12} D_{5m_i} + \beta_{13} D_{10m_i} + \beta_{14} D_{15m_i} + \beta_{15} D_{20m_i} + \beta_{16} D_{25m_i} + \\ & \beta_{17} BA_{5m_i} + \beta_{18} BA_{10m_i} + \beta_{19} BA_{15m_i} + \beta_{20} BA_{20m_i} + \beta_{21} BA_{25m_i} + \\ & \beta_{22} Dsus_{5m_i} + \beta_{23} Dsus_{10m_i} + \beta_{24} Dsus_{15m_i} + \beta_{25} Dsus_{20m_i} + \beta_{26} Dsus_{25m_i}\end{aligned}$$

Slope and aspect for each data point (each tree) were derived using inverse distance weighting in Arc View GIS 3.3. Elevation, DBH, Height (*HT*) and crown length (*CL*) were measured as described in Section 2.1. *IP* is the infestation proportion of the respective circle:

$$IP_{5m_i} = \frac{\sum_{j=1}^{m_{5m_i}} Y_j}{m_{5m_i}} \;,\; IP_{10m_i} = \frac{\sum_{k=1}^{m_{10m_i}} Y_k}{m_{10m_i}} \;,\; IP_{15m_i} = \frac{\sum_{l=1}^{m_{15m_i}} Y_l}{m_{15m_i}} \;,\; IP_{20m_i} = \frac{\sum_{l=1}^{m_{20m_i}} Y_l}{m_{20m_i}} \;,\; IP_{25m_i} = \frac{\sum_{l=1}^{m_{25m_i}} Y_l}{m_{25m_i}}$$

where m_{5m}, m_{10m}, m_{15m}, m_{20m}, and m_{25m} are the number of live lodgepole and ponderosa pine trees with a minimum DBH of 1cm within circles of 5, 10, 15, 20 and 25m of each focal tree *i*. *D* is the density of trees of all species in each circle:

$$D_{5m_i} = \frac{n_{5m_i}}{a_{5m}} \;,\; D_{10m_i} = \frac{n_{10m_i}}{a_{10m}} \;,\; D_{15m_i} = \frac{n_{15m_i}}{a_{15m}} \;,\; D_{20m_i} = \frac{n_{20m_i}}{a_{20m}} \;,\; D_{25m_i} = \frac{n_{25m_i}}{a_{25m}}$$

where $n_{5\mathrm{m}}$, $n_{10\mathrm{m}}$, $n_{15\mathrm{m}}$, $n_{20\mathrm{m}}$ and $n_{25\mathrm{m}}$ are the number of stems of all species in circles with radii of 5, 10, 15, 20 and 25m; $a_{5\mathrm{m}}$, $a_{10\mathrm{m}}$, $a_{15\mathrm{m}}$, $a_{20\mathrm{m}}$ and $a_{25\mathrm{m}}$ are the area of each circle. *BA* is the basal area of each circle:

$$BA_{5\mathrm{m}_i} = \frac{\pi}{a_{5\mathrm{m}}} \times \sum_{s=1}^{n_{5\mathrm{m}i}} \left(\frac{DBH_s}{2} \right)^2, \quad BA_{10\mathrm{m}_i} = \frac{\pi}{a_{10\mathrm{m}}} \times \sum_{t=1}^{n_{10\mathrm{m}i}} \left(\frac{DBH_t}{2} \right)^2, \quad BA_{15\mathrm{m}_i} = \frac{\pi}{a_{15\mathrm{m}}} \times \sum_{u=1}^{n_{15\mathrm{m}i}} \left(\frac{DBH_u}{2} \right)^2,$$

$$BA_{20\mathrm{m}_i} = \frac{\pi}{a_{20\mathrm{m}}} \times \sum_{v=1}^{n_{20\mathrm{m}i}} \left(\frac{DBH_w}{2} \right)^2, \quad BA_{25\mathrm{m}_i} = \frac{\pi}{a_{25\mathrm{m}}} \times \sum_{w=1}^{n_{25\mathrm{m}i}} \left(\frac{DBH_w}{2} \right)^2$$

Dsus is the density of susceptible stems in the circles. I considered trees as susceptible that were live trees of host species (lodgepole or ponderosa pine) with a minimum DBH of 8.2 cm (the minimum DBH of infested trees in these plots):

$$Dsus_{5\mathrm{m}i} = \frac{nsus_{5\mathrm{m}i}}{a_{5\mathrm{m}}}, \quad Dsus_{10\mathrm{m}i} = \frac{nsus_{10\mathrm{m}i}}{a_{10\mathrm{m}}}, \quad Dsus_{15\mathrm{m}_i} = \frac{nsus_{15\mathrm{m}i}}{a_{15\mathrm{m}}}, \quad Dsus_{20\mathrm{m}_i} = \frac{nsus_{20\mathrm{m}i}}{a_{20\mathrm{m}}},$$

$$Dsus_{25\mathrm{m}_i} = \frac{nsus_{25\mathrm{m}i}}{a_{25\mathrm{m}}}$$

where $nsus_{5\mathrm{m}}$, $nsus_{10\mathrm{m}}$, $nsus_{15\mathrm{m}}$, $nsus_{20\mathrm{m}}$ and $nsus_{25\mathrm{m}}$ are the number of susceptible trees within the respective circles.

2.2.2 PARAMETERIZING THE MODEL

The data are correlated in time and space. We fit the model for each plot and year separately to allow for the assumption of temporal independence (Zhu *et al.*, 2005). Nevertheless, the probability modeled is conditional on the values of neighbouring sites; hence, the variance is not constant, exhibiting nonstationarity and heteroscedasticity. It is greater than the theoretical variance expected for a binomial distribution, resulting in "extra-binomial variation" (Dean, 1992). Therefore, we used the pseudo-likelihood method which makes no assumptions of stationarity or homogeneity (Besag, 1975).

Pseudo-likelihood estimates are asymptotically consistent but the variance is inflated, such that a separate analysis for variance estimation was necessary (Nelder & Lee, 1992; Wu & Huffer, 1997).

An extension of the Jackknife technique proposed by Lele (1991) was used for nonparametric estimation of the correct variance-covariance matrix. If possibly dependent variables $(X_1, X_2, \ldots, X_n)$ have a distribution $F(\mathbf{X},\theta)$ then θ can be estimated by a pseudo-likelihood equation,

$$G(\mathbf{X},\theta)=\sum g_i(\mathbf{X},\theta)=\sum_{i=1}^{n}\frac{d}{d\theta}\{\log f_i(X_i|X(N(i)),\theta)\}=0$$

where $N(i)$ denotes the neighbourhood of the site i. Instead of deleting observations of a correlated series, one component of the estimating equation is deleted at a time. Let θ_n be the estimate of the original estimating equation (above) and $\theta_{n,-j}$ the estimate of $G^j(\mathbf{X},\theta)=\sum_{i\neq j} g_i(\mathbf{X},\theta)=0$. The Jackknife estimate of θ is then

$$JK(X_1, X_2, \ldots, X_n)=\theta_n-\frac{n-1}{n}\sum_j(\theta_{n,-j}-\theta_n)=\theta_n-\frac{n-1}{n}\sum_j R_{nj}$$

where $R_{nj}=\theta_{n,-j}-\theta_n$. When the estimation equations are correlated, such that $E(g_i g_j)\neq 0$ for $j\in N(i)$, then the Jackknife estimate of the variance is

$$JKV*\theta_n=(n-1)\sum_{i=1}^{n}\sum_{j\in N(i)}(R_{ni}-\overline{R}_n)(R_{nj}-\overline{R}_n)$$

where $N(i)$ are the sites for which $E(g_i g_j)\neq 0$ and $\overline{R}_n=\left(\frac{1}{n}\right)\sum_j R_{nj}$.

We selected significant variables with a forward selection procedure using a chi-squared test with a significance level of 5%. The low number of infestations in some years caused convergence problems. To increase the sample size, we grouped data from several consecutive years within one plot together that had similar population size. A Wald test with the estimated matrix was performed to determine the relative contribution of each parameter to the variation in the log odds. We performed all analyses with R. Finally, I conducted a linear regression analysis to analyze whether the size of the neighbourhood within which the infestation proportion had a significant effect on the probability of infestation to a tree, increased significantly with beetle population size.

3. RESULTS

3.1 VARIATION AMONG PLOTS

DBH and infestation proportion in the neighbourhood of a tree had the greatest influence on the risk of infestation by MPBs (Table 3-3). The infestation proportion in the neighbourhood of a tree increased the risk to a tree in A, B, E, F and H plots, indicating positive autocorrelation of infestation incidence. The infestation proportion was not significant in G plot, the plot with the smallest population size (Table 3-2). The plots with the largest populations, H plot 2003 and B plot 2005, showed significant effects of infestation proportion in the neighbourhood up to 15 m. E plot 2003 and B plot 2003 which had intermediate infestation rate, showed significance of the infestation proportion in the neighbourhood up to 10 m. Although the populations in A plot and E plot 2004 were much smaller than in the early and post-epidemic years in H plot, infestation proportion significantly influenced risk up to 10 m in A plot and E plot 2004 and only up to 5 m or even absent altogether in H plot. Infestation proportion in F plot 2005 showed a significant effect in circles up to 5 m and up to 20 m.

Table 3-3 Coefficients, P-values and standard errors from the nonparametric jackknife for all variables significantly affecting the probability of attack. Grey shaded cells indicate that these neighbourhoods were not included into the analysis, due to sample size restrictions. Covariates are explained in section 2.2.1. Note that basal area and the density of susceptible trees were not significant. In plots with incipient-epidemic populations sample size was too small to analyze individual years separately. In these cases attacks of all years were pooled together and analyzed as one data set.

	Intercept	Elev.	Aspect	DBH	HT	CL	IP5m	IP10m	IP15m	IP20m	D10m
A plot 2003-2005											
coef.	-13.44	-0.31		0.28				26.86			
Wald	17.22	4.71		7.83				38.38			
P	3.33E-05	3.00E-02		5.15E-03				5.82E-10			
S.E.	3.24	0.14		0.10				4.34			
B plot 2003											
coef.	-12.75				0.32			14.42			
Wald	997.95				187.70			439.87			
P	5.0E-219				1.01E-42			1.15E-97			
S.E.	0.40				0.02			0.69			
B plot 2004											
coef.	-12.38	-2.37	-0.01	0.25							
Wald	41.19	30.28	6.07	13.25							
P	1.38E-10	3.74E-08	0.01	2.73E-04							
S.E.	1.93	0.43	0.01	0.07							
B plot 2005											
coef.	-6.76			0.19					5.04		
Wald	699.84			366.56					169.73		
P	3.2E-154			1.05E-81					8.49E-39		
S.E.	0.26			0.01					0.39		
E plot 2003											
coef.	-8.34			0.18				10.78			
Wald	23.51			10.46				32.38			
P	1.24E-06			1.22E-03				1.27E-08			
S.E.	1.72			0.06				1.90			
E plot 2004											
coef.	-9.76	0.77		0.19				26.24			
Wald	19.28	18.66		9.00				9.51			
P	1.13E-05	1.56E-05		2.72E-03				2.04E-03			
S.E.	2.22	0.18		0.06				8.51			
F plot 2003-2004											
coef.	-20.74	0.62					14.28				29.71
Wald	207.69	76.89					15.03				62.29
P	4.38E-47	1.81E-18					1.06E-04				2.96E-15
S.E.	1.44	0.07					3.68				3.76
F plot 2005											
coef.	-14.20	0.55			0.44		9.09			29.18	
Wald	180.36	17.71			101.15		16.70			17.80	
P	4.05E-41	2.58E-05			8.52E-24		4.38E-05			2.45E-05	
S.E.	1.06	0.13			0.04		2.22			6.92	

	Intercept	Elev.	Aspect	DBH	HT	CL	IP5m	IP10m	IP15m	IP20m	D10m
G plot 2002-2004											
coef.	-7.28	1.16								[redacted]	
Wald	240.22	28.38								[redacted]	
P	3.52E-54	9.95E-08								[redacted]	
S.E.	0.47	0.22								[redacted]	
H plot 2001											
coef.	-6.96			0.11			4.98			[redacted]	
Wald	97.45			24.06			26.67			[redacted]	
P	5.52E-23			9.34E-07			2.41E-07			[redacted]	
S.E.	0.70			0.02			0.96			[redacted]	
H plot 2002											
coef.	-6.41			0.21		-0.08	2.71				
Wald	345.54			317.85		4.79	50.29				
P	3.97E-77			4.26E-71		0.03	1.33E-12				
S.E.	0.35			0.01		0.04	0.38				
H plot 2003											
coef.	-8.27			0.23					6.19		
Wald	535.27			367.12					100.58		
P	2.02E-118			7.94E-82					1.14E-23		
S.E.	0.36			0.01					0.62		
H plot 2004											
coef.	-7.98			0.16			4.94			[redacted]	
Wald	97.81			27.70			55.68			[redacted]	
P	4.61E-23			1.41E-07			8.55E-14			[redacted]	
S.E.	0.81			0.03			0.66			[redacted]	
H plot 2005											
coef.	-8.62	0.43		0.17						[redacted]	
Wald	225.67	38.72		96.17						[redacted]	
P	5.23E-51	4.89E-10		1.05E-22						[redacted]	
S.E.	0.57	0.07		0.02						[redacted]	

DBH increased the risk of infestation in A, B, E and H plots, whereas it was not significant in G and F plot. However, tree height still showed a positive effect in F plot. Crown length was only significant in H plot 2002, where trees with longer crowns were more often infested than trees with short crowns. Elevation increased the risk in G and F plots and in H plot 2005 and E plot 2004. It reduced the risk in A plot and B plot 2004. Aspect was only significant in B plot 2004, where trees with northern aspects were more prone to infestation than trees with southern aspects. Stem density was the only significant neighbourhood variable indicative of competition between trees. It increased the risk of infestation to trees in F plot only. Basal area and density of susceptible trees did not show any significant effects at any neighbourhood size. The intercepts of all models were negative, indicating a threshold of explanatory variables below which the probability of infestation is not greater than 0.

3.2 VARIATION WITHIN PLOTS

Attack rate within the plots significantly increased the distance up to which the infestation proportion in the neighbourhood of a tree affected the infestation risk (Figure 3-2). For example in H plot, the circle delineating a neighbourhood with a radius of 5 m was significant in 2001 when the attack rate comprised 11 infested trees per hectare and also in 2002 when the attack rate comprised 75 infested trees per hectare (Table 3-2). In 2003 attack rate increased to 97 trees per hectare and the effect was significant up to 15 m. In 2004 infestation rate declined to 10.41 trees per hectare with a concomitant decline in the spatial contagious effect of infestation to 5 m distance and eventually the effect was absent in 2005, where only 8.85 trees per hectare were infested. B plot showed the same trend with 25 trees per hectare infested in 2003 and an effect of infestation in the neighbourhood up to 10 m, 7 infestations per hectare in 2004 with no effect of infestation in the neighbourhood and 216 infestations per hectare in 2005 with an effect on the risk of infestation to trees up to 15 m. A and E plots did not exhibit this trend, possibly because the difference in attack rate from year to year was smaller (Table 3-2). The attack rate in early years in F plot showed a significant effect up to 5 m, whereas in 2005, the year of greatest infestation rate in the plot, infestation proportion up to 20 m was significant in addition to the effect up to 5 m.

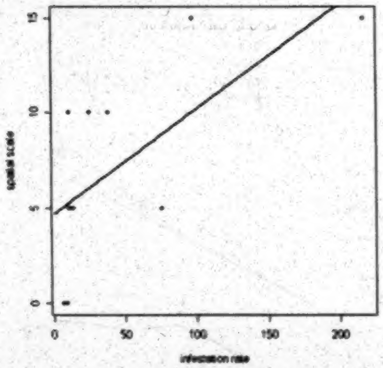


Figure 3-2 The spatial scale of the neighbourhood effect significantly increased with beetle population size. The infestation rate (see Table 3-2) served as surrogate for beetle population. The line shows predictions of the linear regression model scale = 4.690 + 0.055 x infestation rate, where P=0.020 for the effect of infestation rate on the spatial scale of the neighbourhood effect and R^2=0.47.

In most plots DBH was either consistently significant or consistently not significant. In A plot however, DBH increased the infestation risk only in the peak year, where the population of attacking beetles was largest of all years analyzed for that plot. In B plot 2003 height was significant, rather than DBH which was the dominant measure of tree size significant in the following years. Stem density increased the infestation risk in early years of F plot only; it was not significant when the population was larger in 2005 (Table 3-2).

4. DISCUSSION

4.1 VARIATION AMONG PLOTS

Infestation risk of a focal tree increased with the proportion of infested neighbours, most likely because of the switching behaviour of MPBs. It is a typical pattern of MPB outbreaks that once a tree has been infested within a stand other trees nearby are infested over a short period of time (McCambridge, 1967). MPBs utilize pheromone signals to synchronize mass attacks to overcome large trees. Upon feeding on host material beetles produce aggregation pheromones and attract a large number of beetles to the tree so that its defences are soon exhausted (Safranyik *et al.* 1975; Berryman 1976; Raffa and Berryman 1983b; Berryman *et al.* 1989; Pureswaran *et al.* 2000). Once the tree is overcome, aggregation is no longer an advantage. Above 62 females/m^2 bark, larval and pupal productivity declines due to intraspecific interference and scramble competition (Raffa & Berryman, 1983b). To avoid crowded conditions in the host, beetles produce anti-aggregation pheromones (Geiszler *et al.*, 1980; Bentz *et al.*, 1996). Newly arriving beetles are redirected from the focal tree to nearby trees. Another possible mechanism for the attack of neighbouring trees is that increasing concentrations of aggregation pheromones envelope trees nearby (Geiszler & Gara, 1978). Further mechanisms are discussed by Safranyik and Carroll (2006) in greater detail.

Increasing population size consistently led to neighbourhood effects at increasing distances (Figure 3-2). This pattern was apparent among most plots, with the exception of comparisons between H plot with A and E plots. The variability between plots may be due to the fact that pheromones are volatile air borne substances that are distributed by wind. Mark-recapture studies have revealed that wind and temperature strongly affect the beetle's flight direction as well (Safranyik *et al.*, 1989; Safranyik *et al.*, 1992). The inconconsistencies among plots are likely due to variation in wind exposure, local weather regimes and forest structure. The lack of significance for infestation proportion in the neighbourhood of trees in G plot is most likely due to the small infestation rate compared to the other plots (Table 3-2). There may have been a sufficient number of beetles to overcome the defences of weakened trees, but the population may have been too small to produce enough pheromones to attract more beetles. The same argument may explain the absence of the neighbourhood effect in B plot in the year 2004. The decline in the beetle population from 2003 to 2004 is most likely due to emigration of beetles outside the plot (Table 3-2). B plot was located within a continuous forest matrix, so beetles emerging in 2004 may have dispersed outside the plot. In 2005 beetles must have immigrated into the plot from the surrounding stand, as the dramatic population increase could not have resulted from the seven trees that were mass-attacked in 2004.

The finding that infestation proportion had a significant effect on the infestation risk of a tree at different spatial scales in F plot 2005, likely points to the actions of two separate factors. The population in F plot was small (Table 3-2) and yet there was a significant effect of infestation proximity up to 20 m distance, the furthest of all plots. F plot has a different forest structure than the other plots, with greater stem density and more shade-tolerant tree species in the understory (Tables 3-1 and 3-4). Stand conditions affecting the infestation rate may vary at a larger spatial scale than pheromone concentrations.

Table 3-4 Species distribution of trees in over- and understory of in F plot

Species	% of trees smaller than 10m	% of trees 10m and taller
Pinus contorta var. *latifolia*	43.88	89.42
Populus tremuloides	0.70	0.13
Pseudotsuga menziesii var. *glauca*	46.23	8.43
Picea glauca	1.63	0.70
Abies lasiocarpa	7.50	1.27
Tsuga heterophylla	0.06	0.44

Since DBH is correlated with phloem thickness, the critical food resource for MPBs, brood production and survival increases with DBH (Amman, 1969; Cole, 1973; Amman & Pace, 1976; Berryman, 1976; Amman & Cole, 1983). Larger thick barked trees produce the greatest number of beetles (Amman, 1972). Cole (1975) showed that beetles in trees with a DBH of 22.9 - 30.5 cm had a probability of 0.13 for reaching the adult stage, whereas beetles in 38.1 cm trees had a probability of 0.16. Trees with smaller diameters have thinner phloem and are unable to sustain a large number of beetles (Berryman, 1976). The probability of infestation increased only for diameters greater than 14.8 cm in H plot 2003, for example (Figure 3-3). For trees with smaller diameters, the probability of infestation was zero. The large negative intercepts of the models developed here reflect such a threshold relationship.

In addition to the effect of thicker phloem, large trees may affect beetle production in a number of other ways. Large DBH increases the surface area for beetle colonization and multiplication (Safranyik & Vithayas, 1971). Thick bark has more niches in which beetles brace themselves while chewing entrance holes, as MPBs generally attack in bark crevices and under bark scales (Shepherd, 1965; Safranyik & Vithayas, 1971). Thicker bark provides greater insulation against cold in winter (Cole, 1973). Trees with large diameters may also be easier to find in a stand as they appear as a larger silhouette to beetles flying in search of a new host tree (Shepherd, 1966).

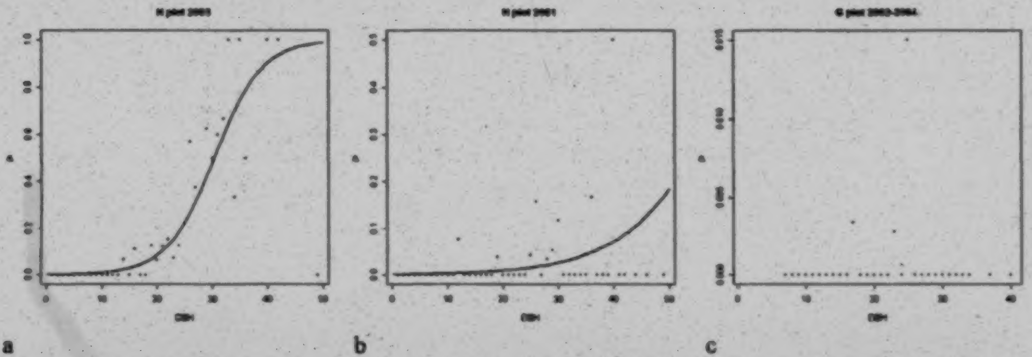
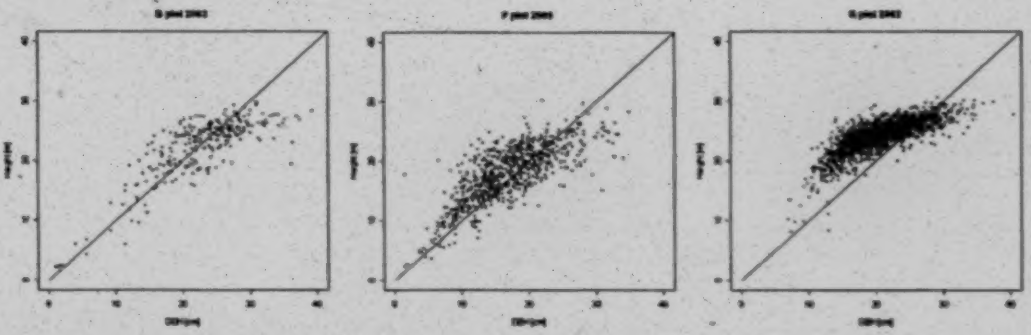


Figure 3-3 Relationship between DBH and estimated probability of infestation. a) DBH significantly increases the probability of infestation π in H plot in 2003 and b) in 2001. c) DBH is not significant in G plot. DBH was divided into intervals of 1 cm. For each interval, empirical π was calculated as the ratio of infested trees to all focal trees with a DBH in the specified interval.

Height significantly influenced the probability of attack in F plot 2005 and B plot 2003, two cases where DBH was not significant. Both height and DBH are complementary measures of tree size and are highly correlated (Figure 3-4). Within a stand, beetles mostly fly in the mid-bole zone above the undergrowth and below tree crowns (Safranyik *et al.* 1989). F plot has a greater density of shade-tolerant trees shorter than 10 m in the understory than any of the other plots (Table 3-1, Table 3-4), such that beetles will fly higher during their search for large lodgepole pine trees and initiate attacks higher up the bole than in other plots. Under such conditions, height may be a better measure of the relevant variation in tree size than is diameter measured at breast height (1.3 m).



a b c

Figure 3-4 Relationship between DBH and height in three plots.

The negative effect of crown length in H plot 2002 is contrary to our expectation, since the population was very large that year (Table 3-2). Crown length, when included independently in the model exerted a significant positive effect on the risk of infestation (coefficient=0.174; P= 1.047e-14; S.E.=0.023, see also Figure 3-5a). In conjunction with DBH, however, the effect of crown length was negative. Within a diameter class, MPBs more often infested trees with short crowns than trees with large crowns (Figure 3-5c).

Infested trees with a DBH greater than 30 cm also have large crowns. This suggests that crown length does reflect nutritional qualities of a tree, but that DBH captures this effect better than does crown length (Figure 3-5b).

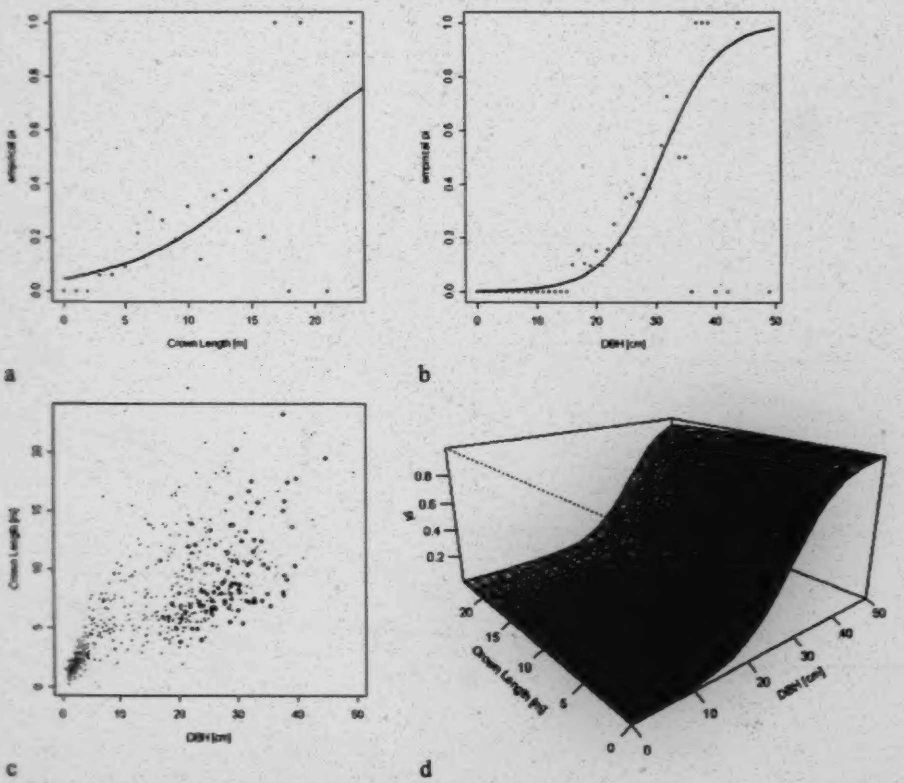


Figure 3-5 Effects of vigour in H plot 2002. a) The risk of infestation as it relates to crown length. The line represents the model $\pi = \frac{e^{-3.03+0.17\times CL}}{1+e^{-3.03+0.17\times CL}}$. Points are empirical values of π calculated as the proportion of infested trees to infested and uninfested lodgepole and ponderosa pine trees within each crown length class of 1m. (b) Empirical values for DBH with predictions of the full model. c) The DBH and crown relationship with large dots representing infested trees. d) Prediction surface based on the full model including DBH and crown length (Table 3-3).

The residual variation in the risk of infestation may be explained partly by a negative effect of crown length, since it affects defence capacity. Crown length determines, in part, a tree's ability to actively metabolize toxins, as photosynthetic capacity increases with leaf area (Christiansen & Ericsson, 1986). Bleiker *et al.* (2003)

found that infested trees had a smaller portion of their boles covered by live crown than uninfested trees. A larger canopy may obstruct landing sites for beetles on the bole. These factors seem to be important even to large populations, although the reduction in infestation risk is very slight (Figure 3-5d). This subtle effect may become significant only when sample size is large. Insufficient sample size may explain the statistically non-significance of crown length in all other plots. It is also possible that there are other factors interacting with crown length that determine a tree's capacity to initiate a hypersensitive response to infestation. Assessment of tree vigour by crown appearance alone, particularly crown length was shown to be unreliable (Kaufmann & Watkins, 1990).

Elevation affects micro-climatic conditions; for example, local areas of increased moisture occur in small depressions and rocky outcrops often cause premature drought conditions. Beginnings of MPB outbreaks were shown to be associated with dry periods with low precipitation (Safranyik *et al.*, 1974; Thomson & Shrimpton, 1984), suggesting that susceptibility changes with moisture gradients. The contrasting effects of elevation on the risk of infestation suggest that relevant micro-climatic conditions may change at a scale different than the one at which it was measured. The finding that in B plot in 2004 trees with northern aspects were more likely infested than trees with southern aspects, may be explained by the negative phototactic and temperature response observed for MPBs (Safranyik & Vithayas, 1971). Southern aspects intercept more light radiation than trees on northern aspects, particularly in a stand with low stem density such as B plot (Table 3-1) (Schmid *et al.*, 1991; Schmid *et al.*, 1992). Greater light interception leads to higher bark temperatures and ambient temperatures than in dense stands.

Stem density in the neighbourhood of a tree increased the odds of infestation only in F plot, the plot with greatest stem density (Table 3-1). Dense stands such as F plot have a greater number of suppressed trees- the most suitable hosts for small populations (Safranyik & Carroll, 2006). Also, in dense conditions, growth in height takes priority over allocation of photosynthates to the production of defensive chemicals, since tree height is crucial for capturing the limiting light resource. When competition is severe, trees maximize fitness by allocating carbon mainly to growth with fewer resources available for storage on the stem and for defence (Kozlowski, 1992; Irwin & Aarssen, 1996; Bonser & Aarssen 1996). Lodgepole pine trees growing in areas of greater density are taller and more slender than trees growing in open areas (Brockley, 2005; Rudnicki *et al.*, 2004). Since resin production is positively correlated with radial growth rate, a tree surrounded by many large trees will have reduced radial growth rates and therefore will also be less resistant to insect infestation (Nebeker *et al.,* 1995; Shrimpton & Thomson, 1983). Basal area was not significant, indicating that the number of neighbours was more important than their size. Depending on the size of the focal tree, thin neighbouring trees may have a significant effect on light interception, whereas nutrient or water uptake would associate more strongly with plant size. The effect of total stem density was more important than the density of susceptible trees, which could simply be due to correlation of the two variables.

4.2 THE EFFECT OF BEETLE POPULATION SIZE

The distance within which infestation rate in the neighbourhood affected the risk of a focal tree depended on the size of the beetle population in the plot. The more beetles, the larger the area within which variation in pheromone concentration may have affected the risk of infestation for the focal tree (Table 3-2, Table 3-3, Figure 3-2). The incipient-epidemic population in G plot did not show significant spatial aggregation, most likely due to the absence of a sufficiently large number of beetles to focus attacks on one patch in the stand. DBH was not significant in G plot, indicating that beetles were restricted by host resistance to trees with smaller DBH.

As a population grows to epidemic proportions there is an additive effect on pheromone production (Raffa & Berryman, 1983b). As the number of infested trees increases, the sources of pheromone plumes increase, attracting more beetles to the stand that will in turn produce more pheromones. This positive feedback results in larger areas affected by pheromones as individual centres of attraction coalesce. The larger the population is, the further the distance from which beetles will be attracted to an infestation hotspot. There are limits to this mechanism, however, as population growth showed a density dependent response in H plot due to host depletion (see below). The small post-epidemic population in H plot 2005 (Table 3-2) did not exhibit a significant spatial effect of infestation in the neighbourhoods (Table 3-3). In addition to the effect of low abundance of resident beetles, the difficulty of locating suitable hosts within the widely dispersed remaining trees may limit spatial correlation. Beetles attracted to focal trees that have already been overcome likely had to fly further to find suitable host trees, increasing the probability of mortality.

The beetles appear to express a different DBH preference as population size changes (Figure 3-3). When population size was very large, the probability of attack rose up to 1 (e.g. H 2003, Figure 3-3a), whereas when the population was not extremely large, the probability of infestation remained low for the entire diameter range of the plot. While even the largest trees were infested in B 2005, H 2002 and 2003, the maximum DBH infested in H plot 2001 was 40.4 cm and most trees with DBH greater than 30 cm remained uninfested (Figure 3-3b). In plots where beetle population was small, DBH was not significant. In G plot, for example, trees with a DBH greater than 25 cm were not infested and the probability of infestation remained very low (Figure 3-3c).

Although trees with large DBH favour beetle reproduction due to their nutritional qualities, they are also more vigorous and have a higher defence capacity. When the beetle population is too small, the cost of overcoming higher defences outweighs the benefits of superior nutritional qualities of more vigorous trees. Per capita offspring may be greater with superior nutrition, but if the tree is not killed and it successfully resists the infestation, beetles are not able to reproduce. When a stress event, such as drought, increases the number of weakened trees available to MPBs for infestation, the population may grow to densities sufficient to overcome stronger defences of larger trees (Safranyik & Carroll, 2006). This allows MPBs to escape competition with secondary bark beetles that do not infest healthy trees. Since MPBs no longer need to share the limited resource of suppressed trees with the secondary bark beetles, the number of trees susceptible to infestation increases as beetles can overcome trees within a greater range of diameters. As productivity is greater in trees with thicker phloem, the population grows until most of the large-diameter trees are killed. The expressed choice of DBH class, therefore, is a result of the balance between nutritional benefits and costs of overcoming defences. The balance will be determined by the beetle density in the stand.

The selection hypothesis predicts that beetles attack large trees first and then attack progressively smaller trees as the host reservoir declines with progression of an outbreak (Klein *et al.*, 1978). DBH remained significant in years after the peak of the outbreak in H plot (e.g. H 2005 Table 3-3 and 3-2). Mitchell and Preisler (1991) showed that once all trees with a DBH greater than 23 cm had been infested, the population crashed. The population in H plot, however, declined before the resource of large trees was depleted. There were still a few trees left with diameters greater than 30 cm, none of which were infested in 2004 or 2005 (Figure 3-6).

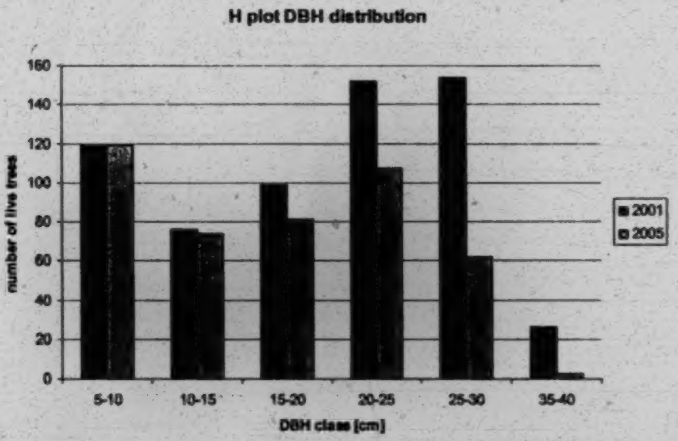


Figure 3-6 Diameter distribution of living trees within H plot before and after the outbreak.

Beetles must have dispersed from the stand to surrounding, uninfested stands. Mortality due to intraspecific competition for remaining host trees may have been high during the peak year. Phloem desiccation due to high attack density and reductions in phloem quality as the host resource declines reduce brood production and survival (e.g. Amman & Cole, 1983). Populations of secondary bark beetle species that do not kill their host and breed in freshly dead wood increase during MPB epidemics as more of their food source becomes available (Safranyik & Carroll, 2006). Interspecific competition for breeding space and direct interference competition also contribute to the decline of MPB populations. Hence, the post-epidemic population in H plot 2005 was again restricted to trees with smaller diameters. The results of this study adds to the selection hypothesis that after the peak of the outbreak beetles select trees with medium DBH due to the reduction in beetle numbers, not necessarily only due to depletion of large diameter trees.

As expected, elevation and aspect were significant only in incipient-epidemic populations. When a beetle population is large enough to infest large diameter trees, but not large enough to attack very vigorous trees, variation in vigour more strongly affects the risk of infestation compared to when the population is large and the beetles are not as severely restricted by their hosts' vigour. The same phenomenon may explain why stem density in the neighbourhood was significant in F plot only for years of small population size (Table 3-2). The reduction in vigour due to variation in microclimate or competition with neighbouring trees will only have a significant effect on populations that are restricted to weakened trees.

5. CONCLUSIONS AND IMPLICATIONS FOR SILVICULTURE

The results of this study point towards determining risk as a function of both stand/tree characteristics and beetle population size. In particular, stand density has been thought to be the major factor for infestation risk. Beetle-proofing, for example, involves spacing trees in order to increase the vigour of individual trees (Larsson *et al.*, 1983). MPB damage has been controlled or at least significantly reduced by thinning stands or growing trees more widely spaced (Cole & Cahill, 1976; McGregor & Oakes, 1987; Mitchell, 1994; Whitehead & Russo, 2005). The positive effect of stem density in the neighbourhood of a tree on its infestation risk supports the use of thinning methods for reducing infestation risk from small resident populations. However, the non-significance of stem density for most plots suggests that thinning may reduce susceptibility only in very dense stands. The photosynthetic rate is greater in thinned stands, which allows for more resources to be allocated to defence. Since crown length had a negative effect on the odds of infestation to individual trees, increasing photosynthetic rate would likely reduce the risk to a stand.

Thinned stands produce significantly more wood than do unthinned plots (Waring & Pitman, 1983) and the primary response to thinning is an increase in DBH (Mata *et al.*, 2003; Brockley, 2005). This may improve a tree's vigour but it also makes it more favourable for the beetles. The outbreak dynamics in the plots studied here suggest that the expressed preference for trees within a certain diameter class reflects a balance of nutritional benefit and level of defence. When beetles are not limited by their capacity to overcome defences, they attack the largest trees available. Beetle proofing will be effective therefore, when populations are small, but if the resident local population is enhanced through immigration from other stands, stands with greater vigour may even be more favourable to a large population than unthinned stands. This prediction is also supported by the fact that the two least dense stands in this study received the highest infestation rates (Table 3-2). Shore and Safranyik (1992) argue that infestation risk cannot be determined by tree and stand characteristics alone and that beetle pressure needs to be considered for accurate risk prediction. Similarly, we emphasize the importance of beetle population size for predicting infestation risk.

Given that the proportion of infestation in the neighbourhood strongly influenced the risk of infestation, it is highly advisable to remove infested trees as soon as possible. When dealing with a high rate of infestation, neighbouring trees within at least 15 m of the infested tree should also be checked for infestation. That is the maximum distance within which the contagious effect of infestation was significant. As soon as one mass attack occurs, a larger population may rapidly aggregate until all large diameter trees have been infested. As discussed above, the success of silvicultural methods for reducing stand susceptibility depends on beetle pressure. Since infestation rate in the neighbourhood of a tree was more significant than density and affected the risk of most stands, the results of this study indicate that the most effective control methods would be those that stifle beetle aggregation.

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CHAPTER 4

INTEGRATING DISCUSSION AND CONCLUSIONS

The two studies presented in this thesis provided insight into dispersal behaviour of MPBs, the dynamic relationships between beetle population size and tree vigour, and population dynamics with host depletion. The studies also provided insights into the advantages and problems associated with different statistical methods.

Results from both provide compelling evidence that infestation by MPB is a contagious process. Point pattern analysis revealed positive association of attacked trees in the plots with typical patch sizes up to 36 m and typically attacked trees occurred within the immediate vicinity of another attacked tree. Autologistic regression analysis suggested that variation in pheromone occurrence was one of the strongest factors determining the probability of attack of a tree, next to DBH. Both patch size and the distance over which the contagious effect of infestation acts on the risk of infestation to a focal tree, increased with beetle population size. The most likely mechanism for these relationships is conspecific attraction of MPBs by means of aggregation pheromones. The more beetles, the more pheromones there will be and the greater the spatial extent of attraction.

However, patch size and the scale of a significant effect on the risk of infestation declined in the later years in H plot. Results suggest a combination of physical constraints imposed by host depletion and behavioural mechanisms may lead to a population decline prior to complete exhaustion of the viable host resource. A greater number of dead trees in years after high infestation rates may inhibit the beetles' ability to focus attacks over large spatial scales since locating suitable hosts is increasingly difficult as they become depleted. Depletion of the frequency of attacked neighbours within the smallest distances from a focal tree showed that depletion rate is greatest in the centre of a patch. Typical distance between attacked trees was greater in later years of an infestation than in the preceding years. The greater difficulty of locating suitable hosts in a stand with high mortality in the previous year may also involve interspecific competition with secondary bark beetles. When infesting trees killed by MPBs, secondary bark beetles generally infest that portion of a bole where MPBs have not established (Safranyik & Carroll, 2006). As their food source increases with the progression of a MPB epidemic, population increase enables them to attack healthy large diameter trees as well. This reduces the amount of breeding space available to MPBs. If a large number of secondary beetles have already infested a tree MPBs may fly on to escape interspecific competition.

MPBs responded differently to host vigour, depending on the size of the population in the plot. At low beetle density DBH did not increase the probability of infestation of a tree significantly because beetles were restrained by the strong defences they would face in large diameter trees. Under such conditions the preferred DBH range is intermediate tree size. For large beetle populations the probability of infestation increases to 1 for trees with very large diameters, although trees with small diameters are attacked as well. At large population size, a tree's defensive capacity is soon exhausted since the rate of beetle attack must be greater when beetle density in a stand is high. Beetles are then no longer restrained by host vigour. This is consistent with a change in spatial pattern from widely dispersed attacks in the endemic state to a highly aggregated distribution under severe epidemic conditions. As more beetles respond to a strong attractive force they are able to infest larger trees. Apart from DBH, few other vigour variables significantly affected the probability of infestation. However, a negative effect of crown length suggests that trees with larger crowns have greater defensive capacities than trees with short crowns. Where understory trees were abundant, height explained more variation in the risk of infestation than DBH. Height and DBH are complementary measures of tree size which determines the quantity and quality of food for the beetles and, thus, also their reproductive productivity.

Stand conditions played minor roles in determining infestation risk. Stem density in the local neighbourhood of a tree increased the risk of infestation, but this effect was only present in a stand where stem density was very high. Indirect effects of density may have caused variation in micro-climatic conditions within and amongst plots that show in a significant effect of elevation. Beetles also showed a negative phototactic response since trees with northern aspects had a greater risk of infestation than trees with southern aspects. This effect was only significant in the stand of lowest stem density, suggesting that stand density may alter the micro-climate of a stand and thereby may indirectly affect the risk of infestation. Micro-climate was most probably also a factor giving rise to a smaller patch size in H plot, despite the large beetle population size. Pheromones disperse differently with increased wind speed, air turbulence and temperature in less dense stands (Whitehead *et al.*, 2004) which may also affect the spatial extent of their attractive effect. Beetle dispersal behaviour will also be affected by variation in micro-climatic conditions.

The detailed stem-mapping technique employed here in conjunction with detailed monitoring of attacks over several years enabled me to study factors that have not been previously addressed in such detail. In particular, my findings stress the importance of beetle population size on pheromone dynamics and host vigour. It is long known that environmental or climatic stress reducing stand vigour is associated with MPB outbreaks (Hopping & Mathers, 1945; Safranyik *et al.*, 1974; Safranyik *et al.*, 1975; Berryman, 1976; Thomson & Shrimpton, 1984; Carroll *et al.*, 2004), and also that weak trees with thin phloem are unable to sustain large epidemic populations (Amman 1969, 1972; Safranyik *et al.* 1974; Berryman, 1976; Amman & Cole 1983). This study showed explicitly how the effect of vigour on the probability of attack to a tree changes as a population increases over time. It revealed that control measures targeted at increasing tree vigour may be a double-edged sword as this may also make stands more favourable to beetles when they are very abundant. Measures to control beetle population sizes may be more effective, although silvicultural measures are important for long-term risk management.

This study also provides new insight into how the dispersal pattern changes with population size. The transition from widely dispersed partially attacked trees in the endemic state to highly aggregated mass-attacked trees in the epidemic phase and eventually to a more random distribution in the post-epidemic phase, was not previously demonstrated, as most studies focus on epidemic populations (McCambridge, 1967; Mitchell & Preisler, 1991; Preisler & Mitchell, 1993; Preisler, 1993; Olsen *et al.*, 1996). These previous studies detected the neighbourhood effect of infestation during epidemics, but no explicit figures were available delineating its extent. The study plots analyzed in this thesis were also larger than those used by Mitchell and Preisler (1991) and related studies. The larger plots enabled identifying patterns over a greater range of spatial scales.

I also provided examples of statistical procedures that may be used for other studies in spatial ecology. The comparisons of results from the *g*-function with those from the *K*-function provide compelling examples that the *g*-function is a very useful complement to the more commonly used *K*-function. Whilst the *K*-function was useful for inferring typical patch size it consistently overestimated the spatial association of attacked trees, due to its cumulative nature. The *g*-function provided more detailed information on the decline in the relative frequency of neighbours with increasing distance class. The subtle relationships between spatial pattern, population dynamics and host distribution would not have been as clear had I only used the *K*-function. Random labelling instead of CSR provided the most appropriate confidence intervals for the hypothesis that trees are attacked at random. Point pattern analysis may thus be a very useful tool in epidemiology and forest health and may go well beyond merely describing a spatial pattern to testing hypotheses on beetle behaviour.

The compelling results indicate that beetles aggregate by means of pheromones, guiding future research in pointing to critical hypotheses to test. Further research is needed to establish a causal relationship between a spatial gradient in pheromone occurrence and the relative frequency of attacked trees. I also identified the scale at which a manipulative study would provide useful insight. Depending on the size of the beetle population, the study area should cover at least the patch size indicated in Chapter 2, i.e. 39 m. A particularly challenging issue for future modelling is identifying methods that contend with the small sample size of endemic and incipient-epidemic populations.

The lack of information on factors determining the behaviour and dynamics of such small populations may simply be due to the difficulties involved with statistical procedures. New methods in spatial ecology and epidemiology need to be developed to underpin conceptual understanding with quantitative assessment of small populations.

Autologistic regression parameterized with the nonparametric Jackknife was effective for analyzing the relative importance of various explanatory variables on the risk of infestation in the presence of spatial autocorrelation. For future research I would use this approach to develop a risk model for high-value stands. Based on the findings in this study, it will include information on beetle population size, tree vigour, stand characteristics and information on the spatial association of attacks. MPB population dynamics at the stand-level may greatly affect the spatial dynamics at the landscape level (Aukema *et al.*, 2006). Hence, it would valuable to couple predictions of infestation occurrence from a stand-level model to landscape-level models, such as the risk rating model developed by Shore and Safranyik (1992) and Shore *et al.* (2000). More data with a finer resolution is required for stand-level models. If the spatial resolution of forest inventory data is not sufficient, resources would need to be optimized to collect data for stands of high economic or social value or where landscape level models predict future outbreaks. The data required for the suggested model could also be used for the Risk Rating Decision Support System developed by Shore and Safranyik (1992, 2006).

The results presented in this thesis also have implications for direct control management strategies. From aerial surveys only red-attack can be detected, i.e. trees infested the previous year (Amman 1982). The result is that not all attacked trees can be detected from visual assessment of the canopy and ground surveys are essential to confirming the extent of infested patches and locating trees currently under attack, i.e. green attack (Wulder *et al.*, 2006). Based on the results from Chapter 2, I recommend that patch sizes estimated from surveys should consider a buffer zone for unobserved green attack. Since typical patch size ranged from 16 m to 36 m, it is likely that most trees affected by the contagious process of attack will be found within 36 m. For stands with lower infestation levels, most trees will occur at smaller distances from mass-attacked trees. Upon detecting attacks, I advise to check trees in the vicinity up to at least 16 m, preferably 36 m if further infestation is to be prevented. The spatial extent of the area examined for additional attacks may be adjusted according to the attack rate. The results from H plot also indicate that a patch that is small in spatial extent may be inhabited by a large beetle population. Patch size alone will therefore not provide accurate estimates of the risk of attack to neighbouring stands. Fixed guideline values that do not account for the spatial pattern of the host may be ineffective. In less dense stands disease spread may have a smaller spatial extent. Therefore, beetle population estimates and surveys should consider the effects stand conditions have on the spatial extent of an infested patch.

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